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Population structure and life history characteristics of fathead minnows, *Pimephales promelas*, in hypoxia-prone Boreal Plains lakes

by

Andy J. Danylchuk ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

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Department of Biological Sciences

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13 August 2003

You never can tell with fish ~ Winnie the Pooh

Imagination is more important than knowledge ~ Albert Einstein

Never stop dreaming ~ Melchizedek

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Population structure and life history characteristics of fathead minnows, *Pimephales promelas,* in hypoxia-prone Boreal Plains lakes" submitted by Andy J. Danylchuk in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology[1].

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13 August 2003

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~ To my father ~

May he somehow see all that I have done.

Abstract

The purpose of my research was to examine the role of natural disturbance (winterkill) in shaping population structure and life history characteristics of fathead minnows, *Pimephales promelas*, inhabiting small lakes in the Boreal Plains. Between 1995 and 1999, my empirical study of four fathead minnow populations showed that densities varied considerably among lakes and years, with dramatic (47-94%) year-to-year declines occurring when dissolved oxygen levels were extremely low in the intervening winter. Large declines occurred in three of four study lakes and two of five years, indicating that winterkill is a pervasive natural disturbance in small lakes in this region. Oxygen levels in a given lake and winter were related to the interactions of lake productivity and depth, local and regional hydrogeology, and the current and antecedent climate; as a result, these local and regional factors strongly influence the natural dynamics of fathead minnow populations in these lakes. Interestingly, in contrast to patterns displayed by larger fish species, smaller individuals were more strongly affected by winterkill than larger individuals.

In comparison to populations in more stable lakes, fathead minnows inhabiting lakes prone to winterkill had shorter lifespans and faster growth rates, grew to a larger size-at-age, particularly at age-0, matured at an earlier age, and allocated a greater proportion of their body mass to gonads. Chronically low population densities in winterkill lakes likely contributed to some of these differences. Results from manipulative experiments conducted in small ponds revealed that the reproductive activity of male fathead minnows can change rapidly, and is modulated by population structure and its affects on social status. These life history traits are consistent with

predictions for organisms in harsh environments, where the selection of plastic phenotypes can increase individual fitness in light of unpredictably high density-independent mortality. In turn, this mortality facilitates population recovery following disturbance via density-dependent effects. Understanding population dynamics of small-bodied fishes resulting from natural disturbance may help explain other natural patterns in northern aquatic ecosystems. Furthermore, since humans can alter factors that influence winterkill, understanding the cascading effects of this disturbance may help us predict the effects of human activities.

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Such an undertaking has definitely been a collaborative effort, and a product of blood [i.e. money], sweat, and tears – some of which were not mine. As for the blood, I gratefully acknowledge the generous assistance of the following organizations who contributed to my work, either financially or through in-kind support: Natural Sciences and Engineering Research Council (NSERC), the Terrestrial and Riparian Organisms Lakes and Streams (TROLS) project and the multitude of organizations that supported this endeavor, Biodiversity Grants Program (Department of Biological Sciences, University of Alberta and Alberta Conservation Association), Canadian Circumpolar Institute, Alberta Sports, Recreation, Parks, and Wildlife Foundation, the WISEST program, The School for Field Studies, and, more recently, The Cape Eleuthera Island School.

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Respect.

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List of Symbols, Nomenclature, or Abbreviations

ANOVA	Analysis of variance
cc	Cubic centimeter
CDD	Cumulative degree days
Chl*a*	Chlorophyll *a*
cm	Centimetre
CV	Coefficient of variation
d	Day
D-L	Discharge on local scale
D-L&I	Discharge on local and intermediate scale
DBA	Drainage basin area
g	gram
G	Gauge
GI	Groundwater interaction
GSI	Gonadosomatic index
F	Female
ha	hectare
km	Kilometre
L	Liter
LM	Large male
LM(R)	Large male, removed
R	Recharge
m	Metre
mm	Millimetre
MBRS	Meanook Biological Research Station
n	Sample size
OR	Otolith radius
SCL	South Calling Lake
SD	Standard deviation
SE	Standard error
SL	Standard length
SM	Small male
TL	Total length
TP	Total phosphorus
TROLS	Terrestrial and Riparian Organisms Lakes and Streams
wk	week
YOY	Young-of-the-year
yr	year
°C	Degrees Celsius
µg	Micrograms

Chapter 1: General Introduction

Introduction

Natural disturbances are discrete events that can greatly influence the distribution and abundance of organisms (Pickett and White 1985; Krebs 1994). For instance, a natural disturbance such as wild fire can cause relatively high mortality simply because abiotic environmental conditions extend beyond individuals' physiological or behavioral abilities to cope with external stressors (Johnson et al. 1998). Natural disturbance can also affect individuals indirectly by changing the availability of resources, such as food or space, which can, in turn, affect how individuals interact with other organisms in their environment (Pickett and White 1985; Winemiller and Rose 1992). As such, the influence of natural disturbance on individuals can cascade through higher levels of organization, leading not only to patterns of distribution and abundance for a particular population, but also to patterns in species assemblages across landscapes (Wiens 1986; Schlosser 1990).

In environments prone to natural disturbance, variation in the distribution and abundance of organisms tends to be a product of the frequency and severity of the dominant disturbance and the traits developed by individuals to contend with stressful conditions (Pickett and White 1985). Too frequent a disturbance or too extreme a change in conditions can result in high density-independent mortality, reducing local populations even to the point of extirpation (Thomas et al. 1994; Hewitt and Butlin 1997). However, at an intermediate frequency or severity of disturbance, physiological and/or behavioral adaptations that have developed in response to the disturbance regime will allow some portion of individuals to persist and contribute to population growth (Winemiller and Rose 1992; Hewitt and Butlin 1997). At lower levels of disturbance, the effects of biotic factors, such as predation or competition, will tend to override the influence of abiotic stochastic disturbance in affecting populations within assemblages (Robinson and Tonn 1989; Reznick et al. 2002). Consequently, population-level traits, such as size or age at maturity, should reflect the historical disturbance regime since only traits that maximize fitness should be selected for (MacArthur and Wilson 1967; Stearns 1992). Therefore, in addition to influencing distribution and abundance, the incidence of natural disturbance should result in variation of life history traits expressed among local populations (Stearns 1992).

In aquatic systems, natural disturbances can have dramatic impacts on fish (e.g., Kushlan 1976; Matthews and Styron 1981). Temporal variation in the physical and chemical properties of water can present physiological and behavioral challenges for fish (Moyle and Cech 1996). Abiotic environmental stressors, including hydrological events such as drought and flooding (Kushlan 1976; Capone and Kushlan 1991; Ostrand and Wilde 2002), extreme temperatures (Sublette et al. 1990; Connolly and Petersen 2003), and changes in dissolved ion and gas concentrations (Matthews and Styron 1981; Moyle and Cech 1996), can all affect fish directly through increased mortality, or indirectly by influencing how fish allocate energy among life history traits to increase their fitness. As such, fish assemblages occurring in areas prone to natural disturbance tend to comprise those species that have developed adaptations necessary to persist and reproduce in these environments (Matthews and Styron 1981; Tonn and Magnuson 1982; Tonn et al. 1995).

The boreal mixed-wood region of western Canada can be characterized as an area of fluctuating, and often extreme, environmental conditions. At the interface between taiga to the north and prairie parkland to the south, the boreal mixed-wood region experiences large seasonal and annual variations in climate (Environment Canada 1999). Such variations, in combination with the post-glacial history and complex hydrogeology of the region (Winter and Woo 1990; LaBaugh et al. 1998), have resulted in a unique and sometimes stressful environment for fish (Nelson and Paetz 1991). Specifically, many lakes in this region are relatively shallow, naturally productive, and poorly drained (Mitchell and Prepas 1990), and these conditions can all contribute to the rapid depletion of dissolved oxygen during the winter (Greenbank 1954; LaBaugh et al. 1998). If oxygen depletion becomes severe, high density-independent mortality, or 'winterkill', of fish can result (Greenbank 1954). Because of variation in the extent of winter hypoxia among lakes, however, as well as species-specific adaptations to these harsh winter conditions, fish assemblages in this region are dichotomous, with lakes prone to this natural disturbance characterized by assemblages of fish species tolerant of severe hypoxia (Robinson and Tonn 1989). In contrast, biotic interactions, notably predation by less tolerant species such as yellow perch, *Perca flavescens*, and northern pike, *Esox lucius*, often exclude the small, hypoxia-tolerant species from lakes less prone to winterkill.

The fathead minnow, *Pimephales promelas*, often dominates the smaller, shallower lakes of the boreal mixed-wood forest (Robinson and Tonn 1989), suggesting that this species is able to cope with periods of severe hypoxia. Nevertheless, if the extent of winter oxygen depletion varies greatly among lakes and years (Barica and Mathias 1979), then winterkill may play a large role in the dynamics of fathead minnow populations in the boreal region. As such, fathead minnows inhabiting boreal lakes of western Canada offer a good model for studying the effects of natural disturbance on fishes since the opportunity to capitalize on whole-lake 'natural experiments' as a study design (Schindler 1998) is relatively great albeit unpredictable. Moreover, given that small lakes in this region are relatively similar in their physicochemical properties and fish assemblage characteristics (Robinson and Tonn 1989), the number and/or magnitude of other factors that could potentially influence population-level traits, independent of disturbance, are reduced, further strengthening the value of the natural experiment approach (Fox and Keast 1991; Reznick et al. 2002). Lastly, fathead minnows are relatively easy to collect and quite hardy, making them amenable for manipulative experiments that can be used to examine mechanisms potentially responsible for patterns observed in natural populations (Diamond 1986).

The purpose of my dissertation research was to examine the role of natural disturbance (winterkill) in shaping the population structure and life history characteristics of fathead minnows inhabiting small lakes in boreal Alberta. The majority of my work involved an empirical study of fathead minnow populations inhabiting four lakes north of Edmonton, Alberta, between 1995 and 1999. These surveys examined how local and regional environmental factors influence the natural disturbance regime responsible for regulating population density and structure (Chapter 2), and, in turn, how differences in the incidence of natural disturbance shape life history traits expressed at the population-level (Chapter 3). In addition, I conducted experiments in small ponds to test how changes in population structure, similar to those potentially caused by winterkill, can affect reproductive patterns in male fathead minnows (Chapter 4). Lastly, I examined the relationship between abundance estimates generated using two different techniques (mark-recapture and catch-per-unit-effort (CPUE)) to determine whether this relationship could be used as a reliable way to rapidly survey remote populations, and potentially increase our ability to examine the effects of natural and anthropogenic disturbance on fathead minnows and other small fishes at larger spatial and temporal scales (Chapter 5). The empirical study of fathead minnows inhabiting hypoxia-prone boreal lakes over 5 years, in combination with manipulative experiments conducted in small ponds and enclosures, shed light on how small-bodied fishes are affected by and respond to winter hypoxia, a natural disturbance characteristically thought to be more stressful to large-bodied species (e.g. Cooper and Washburn 1946; Johnson and Moyle 1969; Casselman and Harvey 1975). Moreover, given that fathead minnows are frequent members of aquatic communities in the boreal region, understanding natural variation in their population dynamics may help explain other patterns in northern aquatic ecosystems, and also help predict the potential effects of anthropogenic disturbance in this region.

Study Species

Systematics and taxonomy

The fathead minnow, *Pimephales promelas*, was originally described by Rafinesque (1820), but until the 1940's, many believed that it was polytypic, recognizing at least three subspecies, *P. p. promelas*, *P. p. confertus*, and *P. p. harveyensis* (Vandermeer 1966; Scott and Crossman 1983). To quantitatively examine trends in systematic traits, Vandermeer (1966) compared meristic and morphometric characters throughout the presumed native range of this species. There was wide variation in traits, and characteristics were clinal and did not vary concordantly, suggesting that classification into subspecies was subjective, both in choosing criteria for taxonomic separation and in delimiting the geographic range of the subspecies (Vandermeer 1966). Moreover, variation in each character was complex, and identifying subspecies would, on the one hand, make the taxonomy unnecessarily cumbersome and on the other, oversimplify the true nature of the phenotypic variation of this species (Vandermeer 1966).

Description

Morphometry: Fathead minnows have a small body, slightly compressed laterally, and a slightly flattened head dorsally. The snout is blunt, with mouth slightly subterminal, strongly oblique to almost vertical, and extending back to below the anterior nostril. Origin of dorsal fin is over to slightly advanced of origin of pelvic fin, and the first ray of the dorsal fin is shorter than the other dorsal fin rays. Fathead minnows express strong sexual dimorphism, which includes differences in morphometry. During the breeding season, males will develop a broader head and a dorsal pad, i.e., prominent area of spongy rugose tissue on the nape, and nuptial tubercles on the snout and lower jaw (Wynne-Edwards 1932; Markus 1934). Females become rotund when bearing large quantities of eggs, and develop a protruding urogenital structure (ovipositor) at least one month prior to spawning (Ficklinger 1969). Ficklinger (1969) noted that there was 3-8% error in distinguishing immature males from females using the presence of the ovipositor.

Pigmentation: Adults are dark brown to dark olive dorsally, have slightly silvery sides and a silvery-white ventral surface. The peritoneum is uniformly black and can often be seen through the belly. Outside the breeding season, both males and females have a narrow dusky lateral stripe extending from the caudal peduncle to the head; this stripe becomes faint to absent in males during breeding season. There is no dark outline on scales (Cross 1967); however, scale pockets above the lateral stripe are edged in pigment whereas scale pockets below lateral line are only slightly pigmented (Becker 1983). Hatchery-reared fathead minnows occasionally exhibit a polymorphism in coloration, with a very small fraction being red, yellow, or white (Robison and Buchanan 1984). During the breeding season, males develop a dark brown to black head, dark body with tan vertical bars on lateral sides, and tan nuptial tubercles (Wynne-Edwards 1932; Markus 1934). Fins of males can become dark and an area of dark pigment forms on the anterior rays of the dorsal fin. Post-larvae have a dark caudal spot and dark pigment at the base of the dorsal fin, which can be used to distinguish post-larval fathead minnows from similar species, such as the bluntnose minnow, *P. notatus* (Buynak and Mohr 1979).

Similar species: Larval and prolarval forms of the fathead minnow are difficult to distinguish from similar phases of bluntnose minnow (Buynak and Mohr 1979); however, Fuiman et al. (1983) provide several practical considerations for identifying fathead minnow larvae using distinguishing morphological characteristics, such as preanal myomere distribution. Fathead minnows and bluntnose minnows also can hybridize, potentially making the distinction between hybrid and non-hybrid individuals difficult (Trautman 1957).

Size, growth, and age: Newly hatched fathead minnows are 4.75-5.2 mm total length (TL) (Markus 1934; Buynak and Mohr 1979; Grant and Tonn 2002), with transformation to early and late postlarval stages occurring at 5.6 mm and 13.6 mm TL, respectively (Buynak and Mohr 1979). Growth is relatively fast, especially in warm, food-rich waters characteristic of more southerly portions of their range (Becker 1983; Scott and Crossman 1983). For instance, Markus (1934) found that fathead minnows in artificial conditions reached adult size within two months of hatching. For a natural population in Wisconsin, Becker (1983) reported that young fathead minnows were able to reach 58 mm TL in 120 days. Although direct examination of growth rates in more northerly natural populations has not been conducted, fathead minnows reared in experimental ponds in Alberta reached only 10-37 mm TL by the end of their first growing season (Grant and Tonn 2002).

Maximum adult size reported for the fathead minnow ranges from 75 to 102 mm TL (McCarraher and Thomas 1968; Scott and Crossman 1983; Robison and Buchanan 1984; Nelson and Paetz 1991), with the mean size for individuals within populations ranging between 50 and 60 mm TL (Carlson 1967; Becker 1983; Scott and Crossman 1983; Sublette et al. 1990). It is commonly observed that males grow more rapidly and to a larger size than females (Andrews and Ficklinger 1979; Becker 1983).

It is regularly stated that fathead minnows rarely exceed age-3 (e.g., Brown 1971), yet only a few studies have directly examined age in this species. One exception is a study conducted by Carlson (1967) using scale analysis, where fathead minnows collected from the Des Moines River, Iowa, were age-1 or age-2, with only one 65 mm TL specimen being classified as age-3. Andrews (1971) subsequently noted a maximum average age of 2.5 years and a relatively small size-at-age for a population at higher elevation, likely coinciding with living in an environment with a shorter growing season.

Distribution, status, and habitat

The fathead minnow is one of the most widely distributed fishes in North America, occurring naturally between the Rocky Mountains and Appalachians, and from Louisiana and Chihuahua, Mexico, to northern Alberta (Brown 1971; Lee et al. 1980; Scott and Crossman 1983; Nelson and Paetz 1991). This species is one of the most common minnows in mid-western states, Ontario, and Canadian prairie provinces (Bailey and Allum 1962; Brown 1971; Nelson and Paetz 1991), but becomes rare or absent in areas of higher elevation or in coastal drainages unless introduced (Jenkins and Burkland 1994). Because of frequent introductions, however, it has been difficult to define the fathead minnow's original distribution in some areas (Etnier and Starnes 1993). For instance, Andrews (1971) reported an altitudinal range extension for the fathead minnow in Colorado, with a self-sustaining population in a mountain lake at 3034 m elevation; however, this population was likely introduced since fathead minnows are not found in any of the major drainages in the region. Similarly, fathead minnows are now found in areas outside of their original geographical range, e.g., western New Mexico and Californian drainages, typically as a result of campaigns to enhance baitfish populations (Bell 1956; Sublette et al. 1990).

Throughout its current distribution, fathead minnows can be found in a variety of waterbodies, including slow moving rivers and streams with emergent vegetation growing in pools or along the shoreline and turbid waters (Starrett 1950; Carlson 1967), prairie pothole lakes and wetlands (Burnham and Peterka 1975; Zimmer et al. 2000), small productive and shallow lakes of the Boreal Plains (Robinson and Tonn 1989; Price et al. 1991), small stained lakes of the Great Lakes region (Scott and Crossman 1983), and many reservoirs and dugouts throughout its natural and current range.

Biology

Reproduction: The reproductive biology of the fathead minnow has been well studied. Fathead minnows can mature rapidly, even at age-0 (Markus 1934); however, it is more frequently reported that individuals mature at age-1 or age-2 (Carlson 1967; Becker 1983). Spawning commences in mid April to early June (Markus 1934; McCarraher and Thomas 1968; Brown 1971; Cooper 1983; Robinson and Buchanan 1984), with exact timing controlled by day length and temperature (Andrews and Flickinger 1979). Spawning begins when water temperatures reach approximately 15ºC, but can be inhibited if water temperatures exceed 30ºC (Andrews and Ficklinger 1979). Reproductive activity ceases in late June to early September (Andrews and Ficklinger 1979).

Males begin to develop secondary sexual characteristics approximately 30 d prior to spawning (Markus 1934), concurrent with the final stages of spermatogenesis (Smith 1978) and early stages of territory acquisition (McMillan and Smith 1974). Prior to spawning, males search for, hold, and aggressively defend nesting sites usually associated with the underside of structure, such as lily pads and downed woody debris (Wynne-Edwards 1932). Fathead minnows also successfully spawn on introduced substrates (Benoit and Carlson 1977), but the use of substrates can be dependent on their size and cardinal location within a waterbody (DeWitt 1993). When defending their territories, males hover below the substrate, making contact movements, such as touching, circling, and rubbing the surface with their dorsal pads (McMillan and Smith 1974). Males will then actively court females through a series of advances and retreats back to their territory. Once a substrate is selected, a female will deposit buoyant sticky eggs on the underside of the substrate using her ovipositor (Ficklinger 1969; McMillan and Smith 1974); egg deposition usually occurs at night (Andrews and Ficklinger 1974).

Once eggs are present in the nest, males become extremely alert, circling the egg mass and boldly charging, butting, and biting potential egg predators (McMillan and Smith 1974), including other small-bodied fishes, and some macroinvertebrates. Conspecifics can also be a high source of egg mortality via egg cannibalism, especially at high population densities when the availability of other foods might be limited (Vandenbos 1996).

In addition to courtship, male aggression towards females has also been suggested to be an adaptation to counteract mimicry of females by deceptive male cuckolders (Jenkins and Burkland 1994); however, this has yet to be formally tested. When piscine predators are present, males adjust their nest guarding activities to be less conspicuous and return time to nests following disturbance increases (Jones and Paszkowski 1997), potentially increasing the susceptibility of predation on eggs and indirectly affecting population size in these assemblages.

Males will continue to guard and care for eggs until they hatch (Andrews and Flicklinger 1979). Care includes agitating the water around the eggs to prevent fouling and keeping them free of sediments, and removing waste material and fungus-infected eggs (McMillan and Smith 1974). A single male may guard the eggs of several females who have deposited them at different times, and Markus (1934) observed from 36 to 12000 eggs per nest. Guarding the eggs of several females may prolong the duration a male remains on a territory, and could affect a male's ability to successfully defend his reproductive space and care for his eggs. Successful males have been shown to maintain a stable body weight throughout the nesting period by continually replacing catabolized energy stores with water, which, in turn, may allow them to deceive potential newly reproductive male intruders and avoid eviction from the nest (Unger 1983). Initially females spawn at random, but then prefer to spawn with males who are already guarding eggs (Unger and Sargent 1988). As such, newly reproductive males will prefer to evict a parental male guarding a nest with eggs rather than occupy a physically identical empty nest space (Unger and Sargent 1988), likely because egg survival has been shown to increase with increasing clutch size (Sargent 1988).

Females are known to be fractional spawners (Andrews and Flickinger 1974; Gale and Buynak 1982), and have been observed to lay from 80 to 480 eggs during each spawning bout (Thomsen and Hasler 1944; Gale and Buynak 1982). Fecundity of age-1 females is reported at 1000-10000 eggs (Andrews and Flickinger 1979; Gale and Buynak 1982). Egg diameter is between 1.1 and 1.3 mm, and the time to hatch is from 4.5-7 d (Scott and Crossman 1983). Burnham and Peterka (1975) found that high salinities in prairie pothole lakes may affect egg and larval survival.

Ecology: The ubiquity of fathead minnows is largely due to this species' ability to tolerate a wide range of environmental conditions (Scott and Crossman 1983). Considered a pioneer species, the fathead minnow is cited as the first species to invade intermittent drainage channels when flooded, and one of the last species to disappear from small, muddy, isolated pools that remain in stream channels during droughts (Cross 1967; Sublette et al. 1990).

With the exception of low pH (Rahel and Magnuson 1983), fathead minnows have been shown to be able to survive relatively extreme water quality conditions. Fathead minnows are often found in plains lakes, where they tolerate relatively high alkalinity (2000 ppm), and salinities of over 10000 ppm (McCarraher and Thomas 1968; Burnham and Peterka 1975; Scott and Crossman 1983). They are also found in drying pools in New Mexico, where they tolerate high water temperatures and low dissolved oxygen levels (Sublette et al. 1990). In addition, fathead minnows have been frequently recognized and well studied for their ability to contend with low oxygen levels during winter months in the northern part of their range (Magnuson et al. 1989).

Fathead minnows possess a number of traits that allow them to survive severe winter hypoxia (Gee et al. 1978; Klinger et al. 1982; Magnuson et al. 1985). The small size of fathead minnows reduces the absolute amount of oxygen needed to support metabolic processes (Klinger et al. 1982). During progressive hypoxia, fathead minnows remain active and move upward in the water column, potentially allowing them to locate areas of higher dissolved oxygen, such as trapped air bubbles or oxygenated inlet and outlet streams (Gee et al. 1978; Klinger et al. 1982; Magnuson et al. 1985). As oxygen levels decline, fathead minnows increase their frequency of opercular movements, likely in an attempt to increase the volume of water flowing across gills (Gee et al. 1978; Klinger et al. 1982). Fathead minnows are also physostomic; however, there is no direct evidence that they are able to use their gas bladder as an accessory respiratory structure (Klinger et al. 1982). Several species of cyprinids, such as goldfish, *Carassius auratus*, and the crucian carp, *Carassius carassius*, have evolved the capacity to switch to anaerobic respiration when exposed to low oxygen levels. They derive energy from the breakdown of glycogen (carbohydrate/glucose carbon) to lactic acid ("glycolysis"), and the accumulated lactic acid is converted to ethanol which then diffuses readily from the gills (Marchand 1987; Holopainen et al. 1997). However, there is no evidence that the fathead minnow has developed such a novel metabolic pathway to contend with winter hypoxia (Shoubridge and Hochachka 1980; Klinger et al. 1982).

In small northern lakes, the structure of fish assemblages in which fathead minnows reside is related to the ability of species to tolerate winter hypoxia, but limited by their ability to tolerate predation (Robinson and Tonn 1989). In Alberta, Ontario, and Wisconsin, there is a dichotomy in small-lake fish assemblages with small-bodied fishes, including the fathead minnow, residing in waterbodies prone to hypoxia, whereas large-bodied fishes, such as northern pike, *Esox lucius*, reside in lakes less prone to this disturbance (Harvey 1981; Tonn and Magnuson 1982; Robinson and Tonn 1989). Although fathead minnows could and do survive in waterbodies less prone to severe winter oxygen depletion, larger, piscivorous fish species restrict their abundance and even presence (Robinson and Tonn 1989; Jones and Paszkowski 1997; Duffy 1998). Thus, when not introduced as forage (see *Importance and Management* below), the fathead minnow is most commonly found in waterbodies devoid of predatory game fish

(Brown 1971). However, when co-existing with predators, the release of chemical alarm substance and associated anti-predatory behaviour of fathead minnows, such as increased shoaling and shelter use, has been shown to increase their chances of survival in laboratory experiments (Mathis and Smith 1993; Chivers and Smith 1994). Interestingly, the closely-related bluntnose minnow co-occurs regularly with piscivorous fish (Tonn and Magnuson 1982).

In the absence of predators, fathead minnows can become important components of small-lake fish assemblages, and may even dominate small-bodied fish assemblages, especially in more depauperate northern areas (Robinson and Tonn 1989; Abrahams 1994). In those small-bodied fish assemblages, the fathead minnow may out compete other species, such as the brook stickleback, *Culaea inconstans* (Abrahams 1996). For instance, the presence of fathead minnows caused a change in the diet, and subsequently reduced growth, of brook stickleback (Abrahams 1996). However, Starrett (1950) suggested that the fathead minnow does not compete well with other minnows in stream environments, potentially based on the species difficulty at feeding in turbulent waters (Landry et al. 1995), suggesting that fathead minnow may only be better competitors in lentic environments.

The life history traits of fathead minnows can be influenced by environmental factors such as water quality, predation and competition. In experimental ponds, nutrient enrichment increased the number of eggs laid and enhanced survival of age-0 fish, contributing to a relatively high number of young-of-the-year (YOY) at the end of the growing season when compared to non-enriched treatments (Grant and Tonn 2002). Despite the higher densities in the cohort, YOY fish were also larger in nutrient enriched treatments (Grant and Tonn 2002), which could have been directly related to higher food rations in the enriched treatment. This contrasts with the results of Vandenbos (1996) in which growth of age-0 fathead minnows was reduced at high age-0 densities in unenriched ponds. Larger YOY appeared, in turn, to increase overwinter survival and recruitment to older age-classes (Grant and Tonn 2002). Differences in predation were also shown to influence the size of fathead minnows, with larger individuals occurring in waterbodies with fewer piscivores (Duffy 1998).

Parasite load in fathead minnows could also affect life history traits, including growth and survival (Lemly and Esch 1984). The infestation of fathead minnows by parasites can be high even when other associated species are only lightly infested (Scott and Crossman 1973). Parasites of fathead minnows include protozoans, trematodes, cestodes, nematodes, and crustaceans (Scott and Crossman 1983). McCarraher and Thomas (1968) noted heavy infestation of cestodes in alkaline lakes in Nebraska, with over 80% of fathead minnows infested with *Ligula intestinallis*.

Diet: The omnivorous fathead minnow is flexible in its choice of foods, feeding primarily on a combination of invertebrates, algae, and detritus. Invertebrate prey include rotifers, cladocerans, copepods, amphipods, ostracods, chironimid larvae and pupae, and ceratopogonid larvae (Held and Peterka 1974; Price et al. 1991; Duffy 1998). Price et al. (1991) found size- and gender-related differences in the types of invertebrate prey consumed prior to the breeding season, likely related to differences in habitat use and activity levels. Duffy (1998) estimated that invertebrate prey consumption can be high, approaching or exceeding estimates of invertebrate production in prairie wetlands.

Landry et al. (1995) found that turbulence in the water column can influence ingestion rate of invertebrate prey by fathead minnow larvae, suggesting that the diet of this species may be partially related to the physical characteristics of the waterbody in which it resides. Alternatively, detritus can contribute up to 93% of the diet of fathead minnows (Litvak and Hansell 1990), and in experimental conditions, fathead minnows whose invertebrate diet was supplemented with detritus showed greater growth compared to those fed invertebrates alone (Lemke and Bowen 1998). Fathead minnows have a long digestive tract that likely contributes to efficient processing of detritus, and thereby permits the extensive use of this poor but abundant food source (Gerking 1994).

Food consumption in fathead minnows can be affected by the risk of predation and interspecific competition with other members of small-bodied fish assemblages. In the absence of yellow perch, *Perca flavescens*, fathead minnows consumed more food than did brook stickleback (Abrahams 1994), suggesting that fathead minnows have a competitive advantage over other small-bodied fishes when predation risk is low. Overlap in diet can also occur between fathead minnows and juvenile ducks, indicating another source of competition that may influence the feeding patterns of fathead minnows (Duffy 1998).

Associated species: Fathead minnows are most commonly associated with other small-bodied fish species (Scott and Crossman 1973; Nelson and Paetz 1991). In the northeastern United States, fathead minnows are associated with species such as bluntnose minnows, *Pimephales notatus*, blacknose dace, *Rhinichthys atratulus*, common shiner, *Luxilus cornutus*, central mudminnow, *Umbra limi*, white sucker, *Catostomus* *commersoni*, and brown and black bullhead, *Ameiurus nebulosus* and *A. melas*, respectively (Cooper 1983). In the northern portions of their range, fathead minnows are commonly associated with brook stickleback, ten-spine stickleback, *Spinachia spinachia*, finescale dace, *Phoxinus neogaeus*, northern redbelly dace, *Phoxinus eos*, and pearl dace, *Margariscus margarita* (Harvey 1981; Tonn and Magnuson 1982; Robinson and Tonn 1989).

Importance and management: Fathead minnows can play an important role in the structure and function of aquatic ecosystems, especially where they occur naturally and in high abundance (Scott and Crossman 1983). For example, Zimmer et al. (2001) found that the re-colonization of a prairie wetland by fathead minnows following winterkill resulted in an increase in turbidity, total phosphorus, and chlorophyll *a*, and a decease in the abundance of some macroinvertebrates. In addition, fathead minnows can act as forage for piscivorous birds (Gingras and Paszkowski 1999), potentially contributing to higher trophic levels; however, few studies have examined the ecological importance of this species (e.g., Janowicz 1999; Zimmer et al. 2001)

More well known is the importance of fathead minnows as forage for game fish, such as largemouth bass, *Micropterus salmoides* (Cross 1967). In fact, in the early 1940's, the intensive collection of fathead minnows from natural systems for use as live bait began to put pressure on minnow stocks and also resulted in the bycatch of YOY game fish (Thomsen and Hasler 1944). As a result, a call was made for "everyone who fishes to realize that minnows are game fish food and that they are, therefore, the foundation upon which fishing is built" (Thomsen and Hasler 1944). Subsequently, these and other authors emphasized the need for artificially propagating fathead minnows (Thomsen and Hasler 1944; Williamson 1944). In the decades to follow, the commercial production of fathead minnows expanded rapidly to meet the demands of the lucrative recreational fishing industry (Bailey and Allum 1962).

Often called ‘tuffy’ by minnow dealers because of its ability to withstand extensive transport and bait bucket conditions, the fathead minnow has become one of the most valuable baitfish in North America (Williamson 1944; Brown 1971; Davis 1993; Etnier and Starnes 1993; Jenkins and Burklead 1994). The ability to mature quickly, willingness to use artificial substrates for spawning, and short incubation period has also contributed to the fathead minnow’s success in aquaculture (Williamson 1944; Brown 1971; Davis 1993). For example, in Arkansas in 1982, the fathead minnow ranked just behind the golden shiner, *Notemigonus crysoleucas*, in importance to the aquaculture industry with over 400 000 kg being produced; this production was valued at nearly two million dollars (Robison and Buchanan 1984). In addition to being used as live bait, fathead minnows are readily stocked by anglers directly into waterbodies as forage fish and into fishless lakes by bait dealers to establish new populations for harvest. Unfortunately, these practices have lead to the introduction of fathead minnows into numerous waterbodies in which they are not native (Bell 1956; Cooper 1983; Robison and Buchanan 1984; Sublette et al. 1990), potentially altering the structure and function of natural aquatic ecosystems.

Several other uses have been found for fathead minnows. Fathead minnows have been stocked into sloughs, ponds, and ditches for mosquito control, and have also been used in sewage treatment ponds to convert high concentrations of nutrient and plant material into usable biomass (Becker 1983). They have been propagated for the aquarium trade, with the development of an ornamental red color morph known as the "rosy red" (Robison and Buchanan 1984). Fathead minnows are also commonly used in the field of aquatic toxicology, being propagated and used in laboratory bioassays and for *in situ* testing of the effects of potentially toxic substances on aquatic vertebrates (e.g., Benoit and Carlson 1977; Brazner and Kline 1990; Siwik et al. 2000).

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Chapter 2: Natural disturbances and fish: local and regional influences on winterkill of fathead minnows, *Pimephales promelas*, in boreal lakes[1]

Introduction

Natural disturbances play important roles in shaping biological communities (Pickett and White 1985). In north-temperate lakes, winter hypoxia is a key natural disturbance that can affect fish assemblage composition (Magnuson et al. 1989; Tonn 1990). Small-bodied fishes have lower oxygen requirements than larger species (Moyle and Cech 1996), and several small-bodied fishes have developed physiological and behavioral adaptations to cope with hypoxia (Gee et al. 1978; Klinger et al. 1982; Magnuson et al. 1985). As such, small-bodied species tend to dominate fish assemblages in lakes prone to winter hypoxia (Tonn and Magnuson 1982; Robinson and Tonn 1989; Tonn et al. 1995).

Variation in the severity of winter oxygen depletion within and among lakes has traditionally been linked to a small set of environmental factors (Greenbank 1945). Local lake characteristics, particularly water depth and productivity, are strongly related to winter oxygen depletion, with shallow, productive lakes being more prone to winter hypoxia than deeper or nutrient-poor lakes (Barica and Mathias 1979). In addition, regional climate patterns can influence the extent of winter oxygen depletion since the duration of ice cover and accumulation of snow can affect the input of oxygen to lakes (Greenbank 1945; Barica et al. 1983). More recently, variation in annual precipitation, in conjunction with a lake's position in the landscape, has also been shown to influence characteristics of lakes that should affect the occurrence of winter hypoxia (Webster et al. 1996, 2000; Devito et al. 2000). For instance, drought can reduce surface- and/or groundwater flow, influencing lake depth and the input of oxygenated water (LaBaugh et al. 1998).

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Although relations between environmental factors and the susceptibility of northern lakes to winter hypoxia have been identified, effects of hypoxia on the population structure and dynamics of resident fishes are much less explored. Even small-bodied fishes that are tolerant of winter hypoxia can be affected if winter oxygen depletion is severe (Klinger et al. 1982). Therefore, differences in winter oxygen depletion among years and lakes may contribute to natural variation in the abundance of small-bodied fishes. In spite of this, no studies have been conducted at appropriate spatial and temporal scales to examine how variation in local and regional environmental factors affect winter hypoxia within and among northern lakes and, in turn, the abundance of resident small-bodied fishes.

In the boreal region of western Canada, lakes are relatively shallow and productive, and often dominated by small-bodied fishes (Robinson and Tonn 1989; Paszkowski and Tonn 2000). This suggests that winter hypoxia is an important natural disturbance in these lakes, and that these systems offer an excellent opportunity to explore the effects of hypoxia on fish population dynamics. To examine such questions, I collected environmental and population data for fathead minnow, *Pimephales promelas* (Rafinesque), inhabiting four lakes in boreal Alberta over a 5-year period. I predicted that fathead minnow populations inhabiting lakes whose local characteristics and regional setting make them vulnerable to winter hypoxia would be more frequently and severely disturbed and show higher variation in abundance and size structure than populations in less susceptible lakes.

Methods

Study Lakes

The four study lakes lie within the Boreal Plains Ecozone, in a roadless area about 200 km north of Edmonton, Alberta (Table 2-1). The lakes were located within 30 km of each other in the Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) project's South Calling Lake (SCL) study region (see Prepas et al. 2001).

The study lakes are all small and relatively shallow (Table 2-1), although SCL20 and SCL100 have steeper basins and thermally stratify during the summer, whereas SCL200 and SCL800 are flat and mixed (Prepas et al. 2001). Despite their geographic proximity, hydrogeologic settings differ among lakes due to spatial variability in the depth and composition of the underlying glacial till and the contour of the bedrock (Devito et al. 2000; Table 2-1). Both SCL20 and SCL800 have one ephemeral surface inflow and are in areas of groundwater recharge, whereas SCL200 has three surface inflows and is in an area of local groundwater discharge. SCL100 is a headwater lake located in an area of both local and regional groundwater discharge; thus, it receives water from beyond, as well as within, the topographical divide of its catchment (Devito et al. 2000). The outflows of all four study lakes are regulated by beaver dams, and immigration or emigration of fish would be likely only when dams collapse.

Fathead minnow dominated fish assemblages of all four study lakes. SCL20 contained an allopatric population of fathead minnow, while the other three populations were sympatric with brook stickleback, *Culaea inconstans* (Kirtland), and finescale dace, *Phoxinus neogaeus* (Cope). In some years, white sucker, *Catostomus commersoni* (Lacepède), would invade SCL200 following collapse of the beaver dam on the outflow; however, gill net surveys indicated that this population was neither persistent nor abundant (Tonn and Danylchuk, unpublished data). No piscivorous fish were present in any lake, and the only visible source of predation on minnows was by piscivorous birds, such as resident common loons *Gavia immer* (all lakes) and red-necked grebes, *Podiceps grisgena*, and irregularly visiting American white pelicans (*Pelecanus erythrorhynchos*).

Population Surveys

I conducted mark-recapture surveys of the four fathead minnow populations annually from 1995-1999. Surveys were carried out in spring, before the onset of reproductive activity. I conducted surveys one lake at a time, alternating the sampling order among years.

I used unbaited Gee minnow traps (2 cm trap openings, 5 mm mesh) to collect fish. The number of traps set in a given lake (10-45 traps) was determined by the number of fish that could be processed in a day. Since fathead minnows in these lakes rarely inhabit water deeper than 2 m (Danylchuk and Tonn, unpublished data), I set traps inshore within the 2-m isobath. Trap locations were determined randomly with the aid of a grid overlayed on a bathymetric map and a random number generator. Traps were set in the late afternoon and retrieved the following day; new trap locations were randomly assigned daily. Fathead minnows > 38 mm (total length, TL), primarily age-1 or age-2 fish and older, were susceptible to the traps (Chapter 3).

All captured fathead minnows were marked by fin-clipping. Because fathead minnows are sexually dimorphic (Flickinger 1969), I marked fish differentially based on gender and maturity (Chapter 4). At the end of each survey (7-9 d per lake), I used the cumulative data to derive abundance estimates for males, females, and juveniles of both sexes using the Schnabel method (Ricker 1975). I derived abundance estimates for each segment of the population separately since this would take into account differential recapture rates among males, females and juveniles and therefore provide more accurate estimates. Abundance estimates for males, females, and juveniles were then summed to provide a total abundance estimate for each population.

To facilitate among-lake comparisons, I converted abundance estimates to densities (#•m^{-3}) by estimating the water volume of the habitat sampled, i.e., the portion of the lakes < 2 m deep, based on bathymetric maps. Densities of males, females, and juveniles were then summed for each lake to provide a total density estimate, with the variance for the summed density estimate being the sum of the variances for each component of the population (Zar 1996). To provide a measure of inter-annual variation in abundance, coefficients of variation (corrected for small sample size; Sokal and Rohlf 1995) were calculated for each population for the five years of our study. To analyze year-to-year changes in fathead minnow abundance within each lake, I calculated the difference between annual estimates and determined whether the difference between consecutive years were significantly different from zero via the Z-test (Zar 1996).

I measured a subsample of 100-200 fathead minnows each day (TL, to the nearest mm). Each subsample was collected from several traps placed around the lake. When catches were low, all fathead minnows from a given trap were used to obtain the subsample for measurement; when catches were high (> 50 fish per trap), I haphazardly measured approximately 25 fish from each trap. From these subsamples, I generated length-frequency distributions for each population in each year. Abundance estimates and length-frequency distributions were then used to determine the numbers of fathead minnows in each size-class. To determine if presumed winterkills were size-selective, I compared the proportion of small (38-58 mm TL) fish before and after large (ca. 50%), statistically significant declines in abundance.

Physical and Chemical Variables

Winter dissolved oxygen profiles (0.25 m intervals) were taken several times per year at the deepest point in each lake as part of the TROLS core monitoring of the SCL study lakes using a YSI model 59 dissolved oxygen meter with stirrer. Because oxygen levels can be spatially variable (Wetzel 2001), I supplemented this monitoring with detailed spatial oxygen surveys in February 1997-1999. Sampling sites for these surveys (n=2-17, depending on lake size, weather, and ice conditions) were selected randomly. I also measured oxygen levels near surface inflows and sites of potential groundwater inflow to determine if oxygen refuges for fish existed. Mean dissolved oxygen concentrations were calculated for each site using the first 0.5 m below the ice-water interface. This stratum is the most oxygen-rich during winter stratification and important for the over-winter survival of fish (Magnuson and Karlen 1970). Since ice and snow conditions can affect oxygen levels in lakes (Greenbank 1945), I also measured ice thickness and snow depth (nearest cm) at each site. To estimate the duration of ice cover, I visited the study lakes at least once a week in fall and spring.

To monitor changes in water levels, I installed staff gauges in the four study lakes in the spring of 1996. Water level was measured in each lake 2-3 times per month between ice-off and early September, and then monthly until ice-on. In 1996, I used changes in water levels between the installation of the staff gauges and the end of the open-water season as a relative indicator of annual change. For 1997 and 1998, I calculated annual change as the difference between the water levels at the ends of the previous and current open-water season. Annual precipitation data were obtained from Environment Canada climate stations within the region.

Euphotic zone water samples were collected about twice per month throughout the open water seasons of 1995-1998 as part of the TROLS core monitoring of the SCL study lakes. I used data for total phosphorus (TP) and chlorophyll *a* (Chl*a*) (see Prepas et al. 2001 for details) as indices of primary production; because of restrictions on data availability, data from 1995 and 1996 are presented as two-year averages.

Data Analyses

Data were tested for normality and homogeneity of variance with Shapiro-Wilkes and Bartlett tests, respectively (Sokal and Rohlf 1995). Fathead minnow density (log (x+1)), and abundance ($\log_{10}$), proportion of small fish (arcsine square root), TP ($\log_{10}$), and Chl*a* ($\log_{10}$) were transformed to meet the assumptions of parametric statistics (Z-test, t-test, ANOVA), and non-parametric methods (Mann-Whitney U test, Kruskal-Wallis test) were used when these assumptions could not be satisfied. For all tests, differences among variables were considered marginally significant if $0.1 \geq P > 0.05$ and significant if $P \leq$

0.05. All statistical analyses were performed using Statistica '99 for the PC (StatSoft Inc., Tulsa, OK, USA).

Results

General Spatial and Temporal Patterns

Abundance estimates for each fathead minnow population were relatively precise, with standard errors ranging from 4 to 20% within a given year. The density of fathead minnows (Figure 2-1) differed significantly among each of the study lakes (ANOVA, $P < 0.001$ and Tukey's HSD). Densities over the 5-year period overlapped between SCL20 and SCL100, and also between SCL200 and SCL800. Within these two pairs, lakes were also similar in their degree of annual variability, with coefficients of variation being lower in the two higher density populations (SCL20 and SCL100) than in the lower density populations (SCL200 and SCL800; Figure 2-1).

SCL20 and SCL100

Winter dissolved oxygen concentrations were consistently higher in SCL100 than in the other study lakes and remained high even when winter conditions were severe (Table 2-2). Correspondingly, the fathead minnow population in SCL100 was the least variable (Figure 2-1), and the size range and frequency distribution of fathead minnows in SCL100 were also similar from year to year, with modes consistently falling between 58 and 62 mm TL (Figure 2-2).

The population in SCL20 was also relatively less variable among years; however, density decreased 47% between 1995 and 1996 (Z-test, $P < 0.01$; Figure 2-1). Although the size range of fathead minnows did not change considerably following this decline (Figure 2-2), the proportion of small fish within the population decreased significantly (t-test, $P < 0.05$). The decrease in density of minnows from 1995 to 1996 corresponded to exceptionally low levels of dissolved oxygen in the intervening winter (Table 2-2). These low winter oxygen levels coincided with the longest duration of ice cover, 222 d, during my study (Table 2-2).

SCL200 and SCL800

The fathead minnow populations in SCL200 and SCL800 displayed the greatest annual variations in density over the course of the study (Figure 2-1), including one and two year-to-year declines of > 60%, respectively. Concurrent with the decrease in density in SCL20, the population in SCL800 decreased by 62% between 1995 and 1996 (Z-test, $P < 0.001$, Figure 2-1). Even more dramatic was the decline between 1998 and 1999, when density decreased by 94% (Z-test, $P < 0.001$). Following both of these declines in SCL800, the proportion of small fish in the population decreased substantially (1995 vs. 1996, t-test, $P < 0.001$; 1998 vs. 1999, Mann-Whitney U test, $P < 0.01$), particularly in 1995-1996, when the length-frequency mode shifted from ca. 50 mm to 68 -72 mm TL (Figure 2-2). Although winter oxygen levels were chronically low in SCL800, dissolved oxygen levels were slightly lower during the winter of 1998/1999 than in previous years (Table 2-2). Unlike the winter of 1995/1996, the duration of ice cover was not prolonged in 1998/1999, however, snow accumulation was high relative to other years (Table 2-2). Moreover, TP and Chl*a* were higher during the open water season of 1998 than in previous years (ANOVA, $P < 0.05$, Tukey's HSD; Table 2-3), indicating increased organic material available for decomposition. Furthermore, precipitation was low in 1998, and water levels were considerably lower prior to ice-on in 1998 than earlier in my study (Table 2-4).

Synchronous with the large decline in density in SCL800, a substantial decrease (> 80%) in fathead density occurred in SCL200 between 1998 and 1999 (Z-test, $P < 0.001$; Figure 2-1). As with SCL800, the length-frequency distribution in SCL200 became skewed towards larger fish concurrent with the decreased density (Figure 2-2), however, this trend was not significant (t-test, $P > 0.1$). Dissolved oxygen levels in SCL200 were below detection during the snowy winter of 1998/1999 and no spatial variation occurred within the lake (Table 2-2). In contrast, spatial surveys in previous winters had revealed considerable heterogeneity in oxygen levels, with concentrations near inlets measuring 4-6 $mg \cdot L^{-1}$. As in SCL800, water level in SCL200 decreased substantially in 1998, when precipitation was low (Table 2-4). This decrease, in combination with an even larger reduction in 1997, owing, in part, to the collapse of the beaver dam on the outlet, resulted in an overall drop in lake level of > 50%. High Chl*a* concentrations were also observed during 1998 (Table 2-3), as in SCL800, reflecting increased production of organic matter.

Discussion

My study suggests that winterkill is a pervasive and common disturbance for small-bodied fish populations inhabiting shallow Boreal Plains lakes. Large density declines followed winters of notably low dissolved oxygen levels in three of the four populations of fathead minnows and in two of five study years. Interestingly, the suite of lakes that experienced winter hypoxia differed between years, indicating that not all lakes in a region respond similarly to regional environmental factors that affect winter oxygen depletion. Fathead minnow populations in two of the study lakes, SCL200 and SCL800, were particularly prone to this disturbance, displaying year-to-year declines of > 80%, correspondingly large coefficients of variation in density and, for SCL800, major shifts in size-frequency distributions; in contrast, populations were less variable in SCL20 and SCL100.

Relative Influence of Local and Regional Factors

I suggest that the extent of winter oxygen depletion and the susceptibility of a lake to winterkill will vary depending on its inherent characteristics and the relative influence of a suite of environmental factors that can be arranged hierarchically from regional to local scales (Figure 2-3). At the regional level, extended duration of ice cover can affect oxygen levels in lakes by reducing atmospheric contributions of oxygen (Barica et al. 1983; Wetzel 2001). Synchronous population declines in SCL20 and SCL800 following the 1995-1996 winter, which had an ice-covered period ca. one month longer than normal, were therefore not surprising. Harsh winter conditions can also be marked by the heavy accumulation of snow and ice cover. Heavy snow and cloudy ice can affect oxygen levels in lakes by reducing photosynthetic contributions of oxygen (Barica et al. 1983; Wetzel 2001). Severe and synchronous winterkills also occurred (in SCL200 and SCL800) following the 1998/1999 winter that provided the heaviest accumulation of snow. Interestingly, this was also a short winter; therefore, predictions of the reduction or elimination of winterkill owing to climate warming that are based solely on winter duration (Stefan et al. 2001) should be viewed with caution.

The importance of regional climate is further illustrated by the synchronous occurrence of winterkill in other lakes in the region during the harsh winters of 1995-1996 and 1998-1999. In three other lakes monitored by the TROLS project, major winterkills of northern pike (*Esox lucius* L.) and white sucker were documented for 1995-1996 (W. M. Tonn, unpublished data). Declines in abundance of other small-bodied species inhabiting the SCL lakes were synchronous to declines in density observed for fathead minnows (Danylchuk and Tonn, unpublished data). Both regional synchrony and a comparable overall frequency of winterkill was documented for an allopatric population of fathead minnows in a small (3.2 ha, 4 m maximum depth) unnamed lake ca. 40 km south of the SCL study lakes (W. M. Tonn, unpublished data). Using methods identical to those employed here, five declines of >50% were documented during 15 years of study of this lake (Figure 2-4). Although winter conditions were not monitored at this site, two of the declines occurred following the winters of 1995-1996 and 1998-1999, synchronously with winterkills in the SCL lakes.

The input and storage of oxygenated water for the winter period, which will influence the probability of winterkill in a lake, is influenced by variation in antecedent precipitation, another largely regional factor, through its effects on local surface and groundwater flow (Webster et al. 1996, 2000; LaBaugh et al. 1998). In my study region, evaporation generally exceeds precipitation (Devito et al. 2000), making the contribution of water from the atmosphere especially important in regulating water flow (Winter and Woo 1990). When precipitation is unusually low, as in 1998, water levels decline and water residence times increase; coincidentally, nutrients and primary production increased in three of my study lakes, likely reflecting reduced water flow and greater internal loading of nutrients (Prepas et al. 2001). In combination with the heavy snow cover of the following winter, these changes in sub-regional conditions likely contributed to winterkill in two of the three lakes. Winter oxygen levels in SCL20 and SCL100 were less affected by the drought because these lakes are deeper, and able to hold more oxygen at the start of winter.

Decreased stream inflows related to regional drought can affect the survival of fish by eliminating oxygen refugia within a lake (Magnuson et al. 1989). Over the course of my study, spatial variation in winter oxygen levels was typically greatest in SCL200, associated with its three small inflowing streams, but this variation was eliminated in the winter following the drought, probably as a result of severely reduced inflows. A lack of winter oxygen refugia may have contributed to the severe winterkill in 1998/1999 as much as the low average oxygen concentrations.

At a sub-regional level, I suggest that the landscape position of SCL100 contributes to its limnological stability and reduced susceptibility to winterkill, relative to other lakes in the SCL region. Since it is in an area of both local and regional groundwater discharge (Devito et al. 2000), SCL100 is less susceptible to changes in water inflow associated with annual fluctuations in climate (LaBaugh et al. 1998) and therefore less susceptible to the drought-related changes in water level, water residency time, nutrient concentrations, and primary production discussed above. Likewise, although SCL200 and SCL800 are both shallow and productive, SCL200's higher lake order and hydrogeologic position in an area of local groundwater discharge likely reduced the extent of winter oxygen depletion and buffered its fathead minnow population from the harsh winter conditions. Correspondingly, fathead minnows in SCL200 did not winterkill during the long winter of 1995-1996 whereas fathead minnows in SCL800 did.

Locally, the morphometry of a lake's basin is known to influence a lake's susceptibility to winter oxygen depletion (Barica and Mathias 1979), but other local factors can play important roles too. The collapse of the beaver dam on the outflow of SCL200, for example, contributed to the dramatic decline in water level in 1997-1998 that, in turn, contributed to the severity of winterkill in 1998-1999. Similarly, a near total winterkill followed a substantial drop in water level when the beaver dam at the outlet of the long-term study pond south of the SCL lakes collapsed in late summer 1986 (Figure 2-4). Clearly, the stochastic nature of beaver-controlled water bodies can influence the incidence of winterkill at a local scale.

Effects on Population Size Structure

The majority of studies on winterkill have focused on large-bodied fish species in north-temperate lakes (e.g., Cooper and Washburn 1946; Johnson and Moyle 1969). The loss of larger individuals from such populations may be related to their larger oxygen demands (Casselman and Harvey 1975). In contrast, I found that populations of fathead minnows that experienced winterkill demonstrated either no size-related trends (SCL200) or substantial decreases in the proportion of small individuals (SCL20 and SCL800). Although I did not sample individuals smaller than ca. 38 mm TL, Magnuson et al. (1985) found that YOY fathead minnows and northern redbelly dace, *Phoxinus eos*

(Cope), emigrated from a hypoxia-prone lake in the fall, whereas adults remained within the lake. This suggests that susceptibility to and effects of winterkill may be different for small-bodied versus large-bodied species. Interestingly, St-Onge and Magnan (2001) found decreases in smaller size-classes of yellow perch, *Perca flavescens*, and white sucker, *Catastomus commersoni*, following disturbances caused by forest fire and timber harvest.

Collectively, my results suggest that large declines in fathead minnow density and shifts in size-structure were related to winter hypoxia. Although I cannot rule out other possible explanations for my long-term comparative study, alternative hypotheses seem much less likely. For example, because smaller fish have lower fat stores and higher rates of energy use than larger fish, smaller fish can be susceptible to over-winter energy depletion (reviewed by Shuter and Post 1990). The large decreases in fathead minnow density in study lakes, however, occurred following both long and short winters. It is also possible that fluctuations in recruitment could have reduced densities and altered population size structure. The likelihood, however, that year-class failures would consistently and repeatedly anticipate critically low winter oxygen levels by 1-2 years (since minnows recruited to my traps at age-1 or 2) seems low. Moreover, it is unlikely that the magnitude of the population declines (47 – 94%) could have been accounted for by year class failure, because these declines involved multiple age-classes (Chapter 3).

Potential implications of human disturbance

Synergistic effects of local, landscape, and regional factors strongly influence winter oxygen depletion and the natural incidence of winterkill for small-bodied fish in

Boreal Plains lakes. Some of these factors can also be influenced by human disturbance, suggesting that the natural risk of winterkill for fishes in northern lakes can be altered by human activities. For example, a reduction in the length of winter resulting from climate warming is predicted to reduce or even eliminate winterkill in shallow north temperate lakes (Stefan et al. 2001). This view, however, considers that the probability of winterkill is largely a function of winter duration, and ignores other local and regional influences such as water level and winter snow pack. In some regions, including western Canada, climate change is also predicted to decrease precipitation in summer and increase evaporation, which can reduce surface and groundwater flow, increase water residency times, reduce lake levels, and increase eutrophication in lakes (Schindler 2001). In spite of a short winter, the most severe winterkills during my study (1998-1999 in SCL200 and SCL800) followed a year of low rainfall that reduced surface flow and lake levels, and increased water residence times and nutrient concentrations. The 1998-1999 winter was also characterized by above-average snowfall, a climatic factor known to affect winter oxygen depletion rates (Greenbank 1945); interestingly, climate change models that predict lower summer precipitation for northwestern Canada also predict moister winters (e.g., Environment Canada 1999). Thus, effects of climate change may actually increase winter oxygen depletion and winterkill in my study region.

The incidence of winterkill could also be affected by human disturbance at the local or landscape level. In addition to enhancing evaporation through greater convection and wind velocity (Schindler et al. 1990), the harvest of timber near lakes could cause an increase in nutrient loading and primary production (Carignan et al. 2000), and, in turn, increase winter oxygen depletion. Land clearing and other activities associated with agriculture can also increase nutrient export to lakes, eutrophication (Cooke and Prepas 1998; Schindler 2001), and therefore the incidence of winterkill for resident fish. Although effects of climate change and other, more direct human impacts on freshwater ecosystems have received considerable attention, those examinations are incomplete if they fail to consider the natural disturbance regime of these ecosystems, and therefore the local and landscape-level factors that affect the frequency and severity of winterkill.

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Table 2-1. Physical characteristics of the four study lakes. DBA = drainage basin area, GI = groundwater interaction (R = recharge, D-L = discharge on local scale, and D-L&I = discharge on local and intermediate scale). Except where noted, data are from the TROLS project core sampling program (see Prepas et al. 2001).

Lake	Latitude (°N)	Longitude (°W)	Surface area (ha)	Volume (10^4 x m^3)	Mean depth (m)	Max. depth (m)	DBA (ha)	Lake order[a]	GI[a]
SCL20	55.18.75	113.65.50	52	250	4.8	12.0	678	1	R
SCL100	55.13.00	111.65.67	18	64	3.5	7.6	292	0	D-L&I
SCL200	55.10.50	113.73.42	109	69	0.6	2.1	5669	3	D-L
SCL800	55.37.50	113.63.00	75	156	2.1	3.0	742	1	R

[a] from Devito et al. (2000)

Table 2-2. Winter conditions for the study lakes (1995-1999). Except for 1995/1996 data, which were collected from a single site/lake in February 1996 as part of the TROLS core sampling program, mean (SD; n) oxygen concentrations are from winter spatial oxygen surveys, collected in February from multiple sites (see text). Ice durations are regional estimates determined from frequent observations during fall and spring. Snow covers are averages from the four study lakes determined during the spatial oxygen surveys.

	Dissolved oxygen (mg•L^{-1})					
Winter	SCL20	SCL100	SCL200	SCL800	Duration of ice cover (d)	Snow cover (cm)
95/96	0.26	3.56	0.12	0.35	222	0
96/97	1.35	6.09	2.84	0.30	201	17
	(0.50;12)	(1.54;12)	(3.32;11)	(0.18;10)		
97/98	4.84	8.32	0.92	0.38	186	21
	(1.65;14)	(0.96;16)	(1.46;17)	(0.25;15)		
98/99	4.18	5.36	0.00	0.28	161	31
	(1.56;8)	(0.06;2)	(0.00;5)	(0.2;7)		

Table 2-3. Mean summer (June-August) total phosphorus (± SE) and chlorophyll *a* concentrations in the study lakes during the period 1995-1998. Data are from the TROLS project core sampling program (Prepas et al. 2001).

	Total phosphorus ($\mu g \bullet L^{-1}$)				Chlorophyll *a* ($\mu g \bullet L^{-1}$)			
Year	SCL20	SCL100	SCL200	SCL800	SCL20	SCL100	SCL200	SCL800
(1995 & 1996)	48	26	47	43	22	11	8	5
	(0.4)	(1.7)	(4.7)	(4.7)				
1997	50	28	56	55	13	23	12	9
	(7.1)	(2.3)	(7.4)	(15.8)				
1998	37	16	77	78	34	6	26	20
	(1.8)	(1.4)	(21.5)	(9.2)				

Table 2-4. Annual precipitation, water residence times, and relative water levels for the study lakes during the 1995-1998 study period. Water residence times were obtained from the TROLS core program (see Prepas et al. 2001). n/a = not available.

	Annual	Water residence time (yr)				Relative annual change in water level (cm)			
Year	precipitation (mm)	SCL20	SCL100	SCL200	SCL800	SCL20	SCL100	SCL200	SCL800
1995	73	5.79	3.32	0.28	3.11	n/a	n/a	n/a	n/a
1996	612	1.41	0.97	0.04	0.89	-2	+7	+26	+18
1997	461	1.65	0.80	0.02	1.11	-15	+6	-38	-2
1998	299	16.49	10.29	0.13	13.46	-29	-12	-27	-33

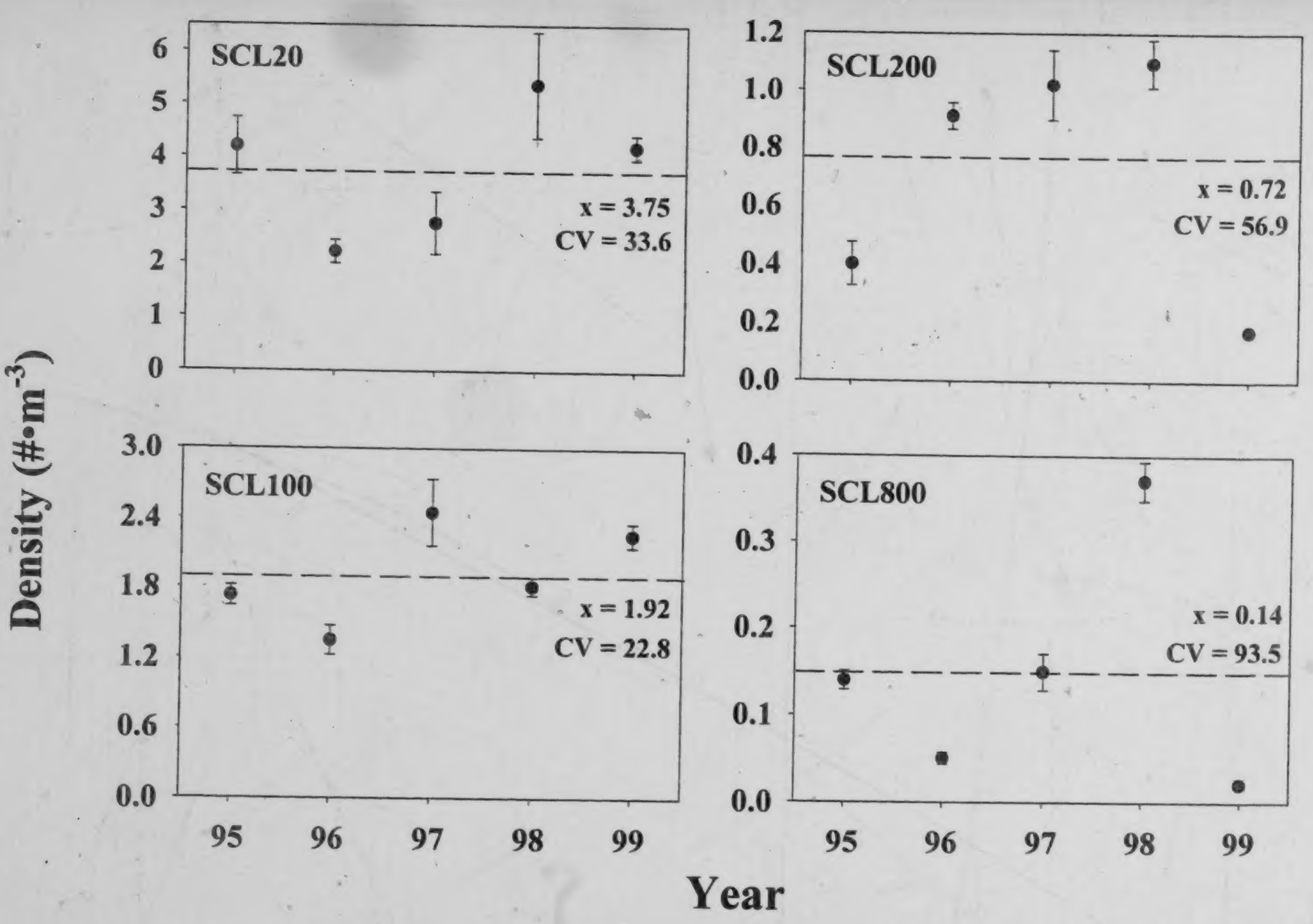

Figure 2-1 Density of fathead minnows (± 1 SE) in the four boreal Alberta study lakes, from spring mark-recapture estimates in 1995 to 1999. Dashed lines represent the mean density for each lake over the course of the study. CV = coefficient of variation (%).

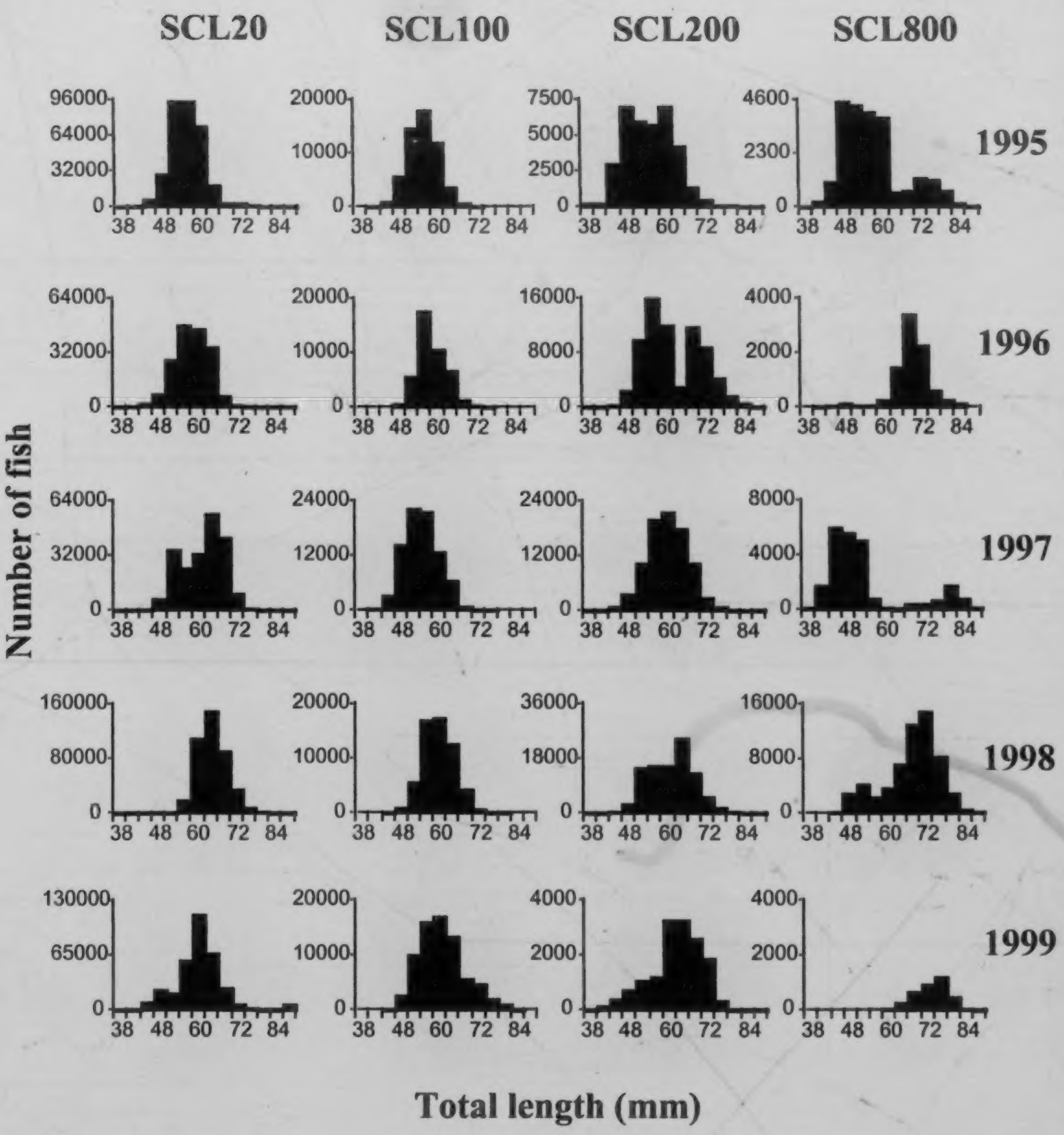

Figure 2-2 Length-frequency distributions for fathead minnows in the study lakes (1995-1999).

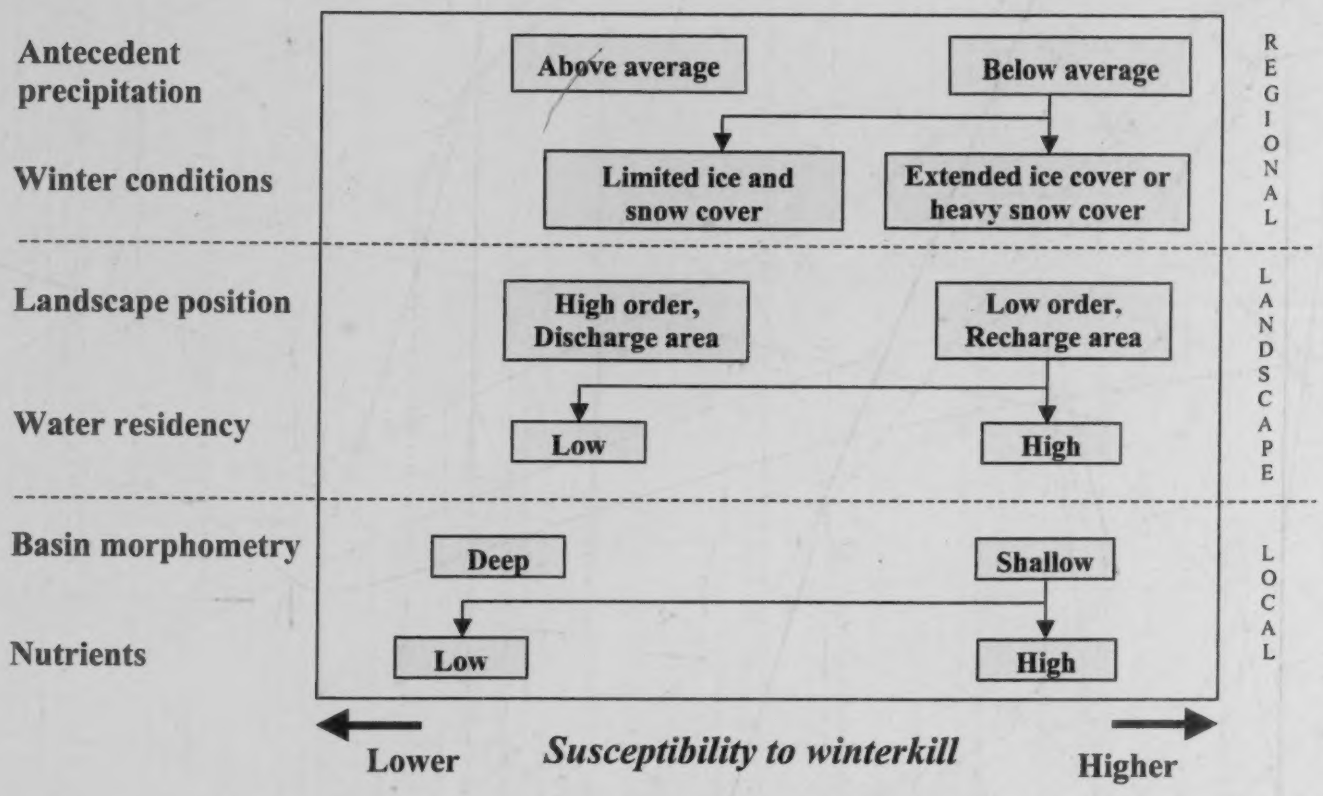
Antecedent precipitation
Winter conditions
Landscape position
Water residency
Basin morphometry
Nutrients
Above average
Below average
Limited ice and snow cover
Extended ice cover or heavy snow cover
High order, Discharge area
Low order. Recharge area
Low
High
Deep
Shallow
Low
High
REGIONAL
LANDSCAPE
LOCAL
Lower
Susceptibility to winterkill
Higher

Figure 2-3 Conceptual model for the relative influence of local, landscape, and regional factors on the susceptibility of a Boreal Plains lake to experience winterkill of fish. Modeled after K. Devito and I. Creed (personal communication; see Buttle et al. 2000).

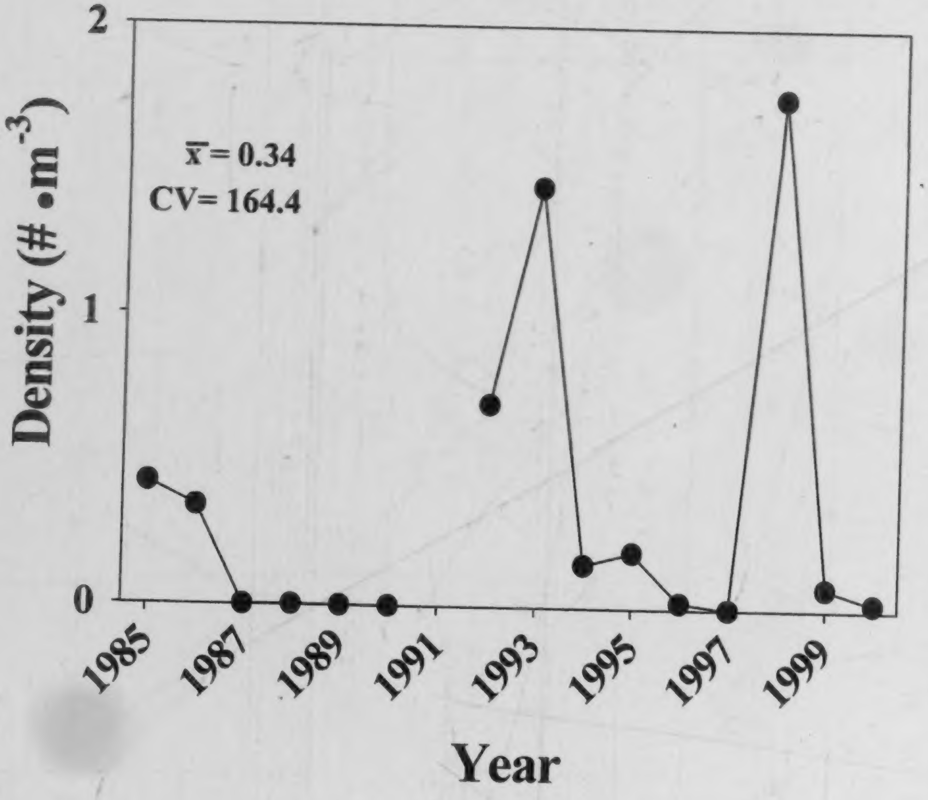

Figure 2-4 Long-term record of fathead minnow densities from a small lake south of the SCL study area. Densities are based on spring mark-recapture estimates from 1985 to 2000 (except 1991). CV = coefficient of variation (%).

Chapter 3: Natural disturbance and life history: effects of winterkill on fathead minnows, *Pimephales promelas*, in boreal lakes

Introduction

Winter conditions in northern regions can decrease oxygen concentrations in lakes. Extended periods of ice and snow cover, which reduce light and therefore photosynthesis, and the decomposition of organic matter, especially in shallow, productive lakes, contribute to the development of winter hypoxia (Greenbank 1945; Barica et al. 1983). In turn, winter hypoxia is a natural disturbance that has dramatic impacts on fish populations and assemblages in north-temperate lakes, including the death, or winterkill, of large numbers of fish when their oxygen requirements are not met (Casselman and Harvey 1975; Tonn and Paszkowski 1986; Fox and Keast 1990).

Absolute oxygen requirements in fish are size-dependent, and larger fish are typically more susceptible to winter hypoxia (Moyle and Cech 1996). As such, winterkill often affects the size structure of populations by reducing the number of large individuals present the following spring (Casselman and Harvey 1975; Fox and Keast 1990; but see Chapter 2). Moreover, because of lower oxygen demands and physiological and behavioral adaptations (Gee et al. 1978; Klinger et al. 1982; Magnuson et al. 1985), small-bodied species tend to cope with winter hypoxia more effectively than large-bodied species. This, in turn, can affect the species composition of fish assemblages, with only small-bodied fishes persisting in lakes prone to winter hypoxia (Tonn and Magnuson 1982; Robinson and Tonn 1989).

Although more tolerant, even small-bodied fishes can be affected if winter oxygen depletion is severe (Klinger et al. 1982). Because the frequency and severity of winter oxygen depletion vary with the limnological characteristics of lakes, population densities and size structures of small-bodied fishes are more variable from year-to-year in lakes prone to severe and/or frequent oxygen depletion than in lakes that develop hypoxia only occasionally, or not at all (Chapter 2). Given the higher density-independent mortality of fish in lakes prone to winterkill and the shorter expected life spans of individuals, life history theory predicts that selection should favor earlier maturity and a higher reproductive investment for these more disturbed and variable populations (MacArthur and Wilson 1967; Stearns 1992). In pumpkinseed sunfish, *Lepomis gibbosus*, for example, populations inhabiting beaver ponds prone to winter hypoxia differed in life history traits from a population in a larger, more stable, lake in the direction predicted by theory (Fox and Keast 1990, 1991). Large environmental differences between beaver ponds and lakes, however, combined with a limited ability of this species to deal with low oxygen levels, likely contributed to the development of different life histories among pumpkinseed populations. It is unknown whether similar differences in life history characteristics hold true among populations of small-bodied fishes, such as minnows, that often dominate small north-temperate lakes. Because, however, small lakes that are less prone to severe winter oxygen depletion are otherwise similar to lake more prone to this disturbance, a more direct examination of the role that winterkill plays in creating and maintaining life history differences is facilitated.

The purpose of my study was to examine the effects of winter hypoxia on life history characteristics of fathead minnows, *Pimephales promelas* (Rafinesque), inhabiting small boreal lakes. I predicted that fathead minnows in lakes prone to winterkill will have a shorter lifespan than populations in lakes where winter oxygen depletion is less severe or frequent. In turn, I predicted that in response to higher adult mortality fathead minnows in the less stable lakes would grow faster, mature earlier, and allocate more resources to reproduction than those in more stable lakes. As well, greater growth and reproductive allocation may permit earlier seasonal timing of reproduction in winterkill populations, which could provide positive feed back favoring greater growth of young-of-the-year (YOY), increasing their overwinter survival and ultimately parental fitness (Post and Evans 1989; Shuter and Post 1990). Conversely, because hypoxia can disrupt endocrine functions in fish and potentially reduce overall reproductive success (Wu et al. 2003), fathead minnows in lakes prone may show reduced different reproductive traits when compared to those in more stable lakes. As such, I also examined seasonal patterns in spawning activity to determine whether differences among populations and other life history traits were linked to the disturbance regime.

Methods

Study populations

The fathead minnow populations in my study inhabited four lakes, accessible only by all-terrain vehicle, located in the Boreal Plains Ecozone of western Canada approximately 200 km north of Edmonton, Alberta (Table 3-1). These lakes, designated SCL20, SCL100, SCL200, and SCL800, are located within 30 km of each other, and are <110 ha in area, 0.6 to 4.6 m in mean depth, and naturally eutrophic (Table 3-1; see Devito et al. 2000 and Prepas et al. 2001 for limnological details). Small-bodied species dominate the fish assemblages of the four lakes. SCL20 contains an allopatric population of fathead minnow, while the other three lakes are inhabited by fathead minnow, brook stickleback, *Culaea inconstans* (Kirtland), and finescale dace, *Phoxinus neogaeus* (Cope). In some years, SCL200 also contains a small, transient population of white sucker, *Catostomus commersoni* (Lacepède).

I studied the four populations of fathead minnow from 1995-1999. Population estimates derived from mark-recapture surveys showed that densities varied greatly across populations, as did the degree of year-to-year variability (Table 3-2; Chapter 2). Variability among lakes and years was largely driven by the extent of winter oxygen depletion, as large declines in fathead minnow density (47-94 %) were documented in lakes following winters of notably low dissolved oxygen levels. These winterkills occurred at least once in three of the populations and in two of the four winters (Table 3-2), indicating that winterkill is a common natural disturbance for fathead minnows in this region; nevertheless, individual lakes differed in the frequency and severity of this disturbance.

Of the four study lakes, SCL800 and SCL200 experienced the most dramatic (>80%) and/or frequent overwinter declines in fathead minnow density. The population in SCL20 experienced one significant decline (47 %), while the population in SCL100 was less variable from year to year (Table 3-2). Thus, the four populations represent a gradient of populations at risk of winterkill, from high (SCL800) to low (SCL100); this gradient was well reflected in the coefficients of variation in population density over the five years (Table 3-2).

Life history characteristics

From 1995 through 1998, I used unbaited Gee minnow traps (2 cm trap openings, 5 mm mesh) to collect fathead minnows from each lake early in the spring, shortly after ice-off and before the onset of reproductive activity. Fish > 38 mm (total length (TL)) were susceptible to the traps. Traps were set in the late afternoon at randomly selected sites within the 2-m depth stratum where fathead minnows concentrate (Danylchuk and Tonn, unpublished data), and retrieved the following day. I euthanized a subsample of approximately 60 fish per lake and year with tricaine methanesulfonate (MS 222), stored them on ice, and subsequently froze them.

After thawing with cold tap water, fish were measured (TL to the nearest mm), and weighed wet (to nearest 0.001 g). To determine gender and stage of maturity, I dissected all specimens and assessed the physical condition of the gonads via macroscopic observation. Fish were considered mature if testes were white and enlarged or ovaries contained yolked eggs. Gonads were removed and weighed (nearest 0.001 g). Both lapilli otoliths were also removed, cleaned, and stored dry until they were processed for aging.

To prepare otoliths, each lapillus was mounted whole on a glass microscope slide. The slide was warmed on a hot plate (45-55 C) and a thin layer of thermoplastic cement (Buehler No. 40-8100) was applied to one end of the slide. Once the cement thickened, one otolith was placed in it with the convex lateral surface facing up. After cooling, I ground otoliths using a sequence of progressively finer wet sandpaper (600, 1200, and 1500 grit) until the primordium was clearly visible. Lapilli were then polished with diamond paste (8000 mesh equivalent) and a felt polishing cloth. I then reheated the slide and spread a thin layer of molten thermoplastic cement over the otoliths as a clearing agent.

Otoliths were examined in transmitted light at 20 x magnification and measurements were made with an ocular micrometer. The otolith radius (OR) and distance to each annuli were measured using a longitudinal axis from the primordia to the posterior edge of the otolith. For each population, I determined a standard TL-OR relationship by linear regression using fish collected during all study years (sample sizes for each population ranged from 160-198 fish). Using the standard TL-OR intercepts for each population, I back-calculated the length at age for each fish via the Fraser-Lee method (Bagneal and Tesch 1978). I then determined the mean back-calculated TL for each age and calculated instantaneous growth rates [ln(TL at age x+1) - ln(TL at age x)] between consecutive ages for each sex to quantify age-specific growth patterns in each population. Instantaneous growth rates between age-0 and age-1 were calculated using size-at-hatch (5.44 mm TL) for TL at age-0 (Kiesling 1999).

As a measure of body condition, I examined the relationship between body mass and TL for males and females in each year, and compared the standardized slopes for each sex to test for differences in body condition across populations. The proportion of mature fish at each age was determined for each sex and compared across populations. For each mature fish, I calculated the gonadosomatic index (GSI; (gonad weight/body weight) x 100) as a measure of energy allocated to the development of testes or ovaries.

Reproductive activity

During the breeding season, reproductively active males establish territories around the underside of structures, including introduced nesting substrate (Wynne-Edwards 1932; Andrews and Flickinger 1974; Benoit and Carlson 1977), and subsequently fertilize and care for the eggs that are laid on the structure by females. I monitored reproductive activity from 1996 to 1998 by deploying as nesting substrate 12-16 floating fence boards (100 x 4.5 cm) anchored to bricks along the shoreline of each lake (see Chapter 4 and Grant and Tonn 2002). Nestboards were placed in groups of 3-4 in the north, south, east, and west ends of each lake, with nestboards in each group approximately 20 m apart. To estimate the date spawning activity was initiated in each lake, I checked nestboards every 2-3 d beginning just after ice-out, for the presence of eggs. Following the initiation of spawning, I checked nestboards approximately every 7-10 d, recording the number of nests on each nestboard, and assessing egg development. From these observations, I estimated peak spawning activity and duration of the reproductive season for each population in each year. Peak spawning was marked as the date with the highest mean number of nests per nest board for each population. The duration of the spawning season was estimated by determining the number of days between the initiation of spawning activity and the date of the last survey when eggs were present on nestboards. I stopped monitoring the nestboards when no nests were present for two consecutive sampling periods.

Because water temperature can effect the initiation of reproduction (e.g., Ridgway et al. 1991), I deployed a temperature data logger (Hobo 8K, Onset Computer Corporation, Pocasset, MA, USA) in each lake shortly after ice-out in each year. Loggers were set in ca. 30 cm of water at the north end of each lake. Water temperature was recorded hourly throughout the open water season, and the thermal regime of each lake in each year was characterized by calculating cumulative degree-days ≥15°C, based on mean daily temperatures. Cumulative degree-days ≥15°C were used because this temperature represents a liberal estimate of the mean minimum water temperature at the initiation of spawning activity for fathead minnow (Andrews and Flickinger 1974). From these data, I determined the mean cumulative degree-days at initiation of spawning for each population to test whether population-level differences in the initiation of spawning activity was related to lake-specific differences in thermal regime.

Data analyses

Data were tested for normality and homogeneity of variance with Shapiro-Wilk and Bartlett tests, respectively (Sokal and Rohlf, 1995). Back-calculated TL at age-3 ($\log_{10}$), proportion mature (arcsine square root), and GSI (arcsine square root) were transformed to meet the assumptions of parametric statistics (t-test, ANOVA), and non-parametric statistics (Mann-Whitney U test, Kruskal-Wallis test) were used when these assumptions could not be satisfied. For all tests, differences among variables were considered marginally significant if $0.1 \geq P > 0.05$ and significant if $P \leq 0.05$. All statistical analyses were performed using Statistica '99 for the PC (StatSoft Inc., Tulsa, OK, USA).

Results

Age, growth, and body condition

Maximum age of fathead minnows was highest (5+ years) in the least variable populations, SCL100 and SCL20, and lowest (3+ years) in the most disturbed and variable population, SCL800 (Figure 3-1). The only difference in longevity between sexes occurred in SCL800, where males lived one year less than females (Figure 3-1). Because of relatively large variation, size-at-age did not differ between sexes (t-test or Mann-Whitney U, $P>0.1$) except for age-5 fish in SCL 20 and SCL100, and age 2 fish in SCL800; in those cases, males were larger than females (t-test, $P<0.05$). Given those few differences, I combined the back-calculated size-at-age for both sexes to examine general trends for the entire population (Figure 3-1).

Maximum size and size-at-age displayed the opposite pattern relative to longevity; fathead minnows in SCL800 had the fastest growth and achieved the greatest mean TL (75 mm), followed by fish in SCL200, SCL20, and SCL100 (Figure 3-1). Mean length-at-age was significantly different among populations for ages-1+, 2+, and 3+ (Kruskal-Wallis or ANOVA, $P<0.05$). Fish of these ages in the two less variable populations, SCL20 and SCL100, were smaller than fish in SCL800 (Mann-Whitney U or Tukey's HSD, $P<0.05$). Fish in SCL100 were also smaller at age-1+ and age-2+ than similar-aged fish in SCL200 (Mann-Whitney U, $P<0.05$). In turn, age-2+ and 3+ fish in SCL200 were smaller than fish of comparable ages in SCL800 (Mann-Whitney U, $P<0.05$).

For both sexes, age-specific growth rates differed among populations between ages-0 and 3 (ANOVA or Kruskal-Wallis, $P<0.05$; Figure 3-2). During their first year of life, fathead minnows in SCL200 and SCL800 grew faster than conspecifics in SCL20 and SCL100 (Mann-Whitney, $P<0.05$). These differences were maintained in their next year for males (Tukey's HSD, $P<0.05$), however, females differed only between SCL800 and SCL100, with those in the former lake growing faster (Tukey's HSD, $P<0.05$). Between age-2 and 3, males and females in SCL20 and SCL200 grew faster than those in SCL100 (Mann-Whitney, $P<0.05$); faster growth for these age-classes also occurred for females in SCL800 when compared to females in SCL100 (Mann-Whitney, $P<0.05$).

Although body condition of males appeared higher than females in all populations (Table 3-3), sexes differed only in SCL800 (t-test, $P<0.05$). Condition did not differ across populations for either males or females (ANOVA, $P>0.1$).

Reproductive traits

The proportion of mature individuals at each age was relatively high across all populations for both sexes (Figure 3-3). A higher proportion of males were mature at age-2 in SCL200 and SCL800 when compared to fish of similar age in SCL20 and SCL100; however, differences were not significant among populations (Kruskal-Wallis, $P>0.1$). Similarly, the proportions of mature females at age-2 in SCL200 and SCL800 were slightly higher than the proportion in SCL20; however, the proportion of mature age-2 females in SCL20 was still high.

Across populations and years, mean GSI ranged from 0.7 to 6.8% for males and from 4.1 to 23.0% for females. GSI differed across populations for both males and females (ANOVAs, $P<0.01$). Both males and females in SCL800 had higher GSI than fish in SCL20 and SCL100 (Tukey's HSD, P<0.05; Table 3-3), whereas females in SCL200 also had higher GSI than those in SCL100 (Tukey's HSD, P<0.05).

Based on the monitored nestboards, nesting activity began between mid-May and early-June (Table 3-4). The initiation of spawning activity did not differ among populations (ANOVA, P>0.1), even though fathead minnows in SCL200 and SCL800 appeared to initiate spawning activity 1-2 wk earlier than conspecifics in SCL20 and SCL100. Similarly, spawning activity in SCL200 and SCL800 began with fewer cumulative degree-days ≥15°C, but differences among populations were only marginally significant (ANOVA, P=0.1). Although spawning activity appeared to peak earliest in SCL200 and SCL 800 (Table 3-4), differences among populations were not significant (ANOVA, P>0.1). The duration of spawning activity also did not differ among populations (ANOVA, P>0.1).

Discussion

Life history traits of fathead minnow varied among populations, and differences were related to the incidence of natural disturbance. Fathead minnows in lakes prone to frequent and/or severe winterkills were shorter lived, exhibited faster growth rates, grew to a large body size at age, allocated a greater proportion of their body mass to gonad development, and tended to mature earlier compared to fathead minnows in more stable lakes. In addition, spawning activity began somewhat earlier in the season in lakes prone to severe winter hypoxia.

As a natural disturbance, winterkill directly removes individuals from a population; not surprisingly, densities in lakes prone to frequent or severe winterkill were lower than those in lakes less subject to this disturbance (Chapter 2). In turn, population density, through its effects on per capita resource availability, could influence opportunities for the uptake of energy to be allocated to the competing ends of maintenance, growth, and current reproduction (Murnyak et al. 1984; Deacon and Keast 1987). For example, Deacon and Keast (1987) found that pumpkinseed sunfish grew to a large body size and had higher reproductive output in a lake with lower population density and higher prey availability than did conspecifics inhabiting a lake with higher population density and lower prey availability. Although a concomitant increase in both growth and reproduction seems contrary to the idea of trading-off energy among life history traits, the costs of allocating resources from one trait to another may only be incurred when energetic resources are limited (Schultz and Warner 1991). In my study, food resources may not have been limited in lakes prone to winterkill because of lower population density and higher invertebrate biomass (see Prepas et al. 2001), allowing greater allocation of energy to both growth and reproduction by fathead minnows. Moreover, differences in growth among my study populations were largely established within the first year of life, indicating that differences were likely related more to density and resource availability than a trade-off of energy between growth and current reproduction.

In conjunction with lower density and higher per capita resource availability, differences in first-year growth rates could also be linked indirectly to densities through the timing of reproduction. Given that the seasonal timing of reproduction in fish can be positively size-dependent (Ridgway 1991; Danylchuk and Fox 1994, 1996), the larger body size of fathead minnows inhabiting lakes prone to winterkill may have allowed an allocation of energy to reproduction earlier in the season relative to smaller fish inhabiting more stable lakes. In turn, spawning early in the season could contribute to the larger body sizes of YOY in winterkill lakes by providing offspring more time to accumulate energy, especially if competition for food resources within a cohort is low (Post et al. 1999).

The timing of reproduction within an individual's lifetime could also be affected by the susceptibility to winterkill through its influence on lifespan. Individuals with relatively different lifespans should adjust their age at maturity to increase the likelihood of contributing young to the next generation and maximize parental fitness (Stearns 1992; Gunderson 1997). The trend of an earlier age at maturity observed for populations more prone to winterkill is likely a response related to reduced lifespan associated with the high adult mortality caused by of this disturbance (Fox and Keast 1991). A similar response in age at maturity can be invoked by predator-induced mortality (Reznick 1996); however, the major predators in my study lakes are piscivorous birds, such as the common loon (*Gavia immer*). Given that piscivorous birds were present on all four lakes, the incidence of predation was likely not a factor here.

Clearly, winter hypoxia is a strong environmental disturbance that can help shape the life history characteristics of fathead minnows in boreal lakes, and the patterns I observed among populations are consistent with predictions for organisms living in unpredictable environments (Stearns 1992). In spite of the close proximity of the four populations and the generally similar limnological characteristics of the lakes in which they reside, the frequency and severity of winterkill among the four populations varied, which then had concomitant effects on life history traits. Because a greater frequency or intensity of winterkill will reduce lifespan in some populations, the differences in life history traits I observed may be related to microevolutionary selection that influences the trade-off of energetic resources throughout the course of an individual's lifetime (Stearns 1992; Van Winkle et al. 1993). However, because the extent of winter hypoxia varies dramatically and unpredictably from year to year, the evolution of more flexible, or plastic phenotypes can also result (Stearns 1992; Belk 1995; Baker and Foster 2002).

The ability of fathead minnow populations to persist in highly variable and unpredictable environments, not only in the boreal forest but throughout their wide geographic range (Scott and Crossman 1983; Sublette et al. 1990), suggests that selection has favored the evolution of phenotypic plasticity (Stearns 1992). Empirical studies such as mine that compare and contrast the expression of life history traits among populations exposed to different, and varying, environmental conditions are critical to identify the phenotypic traits that are variable and likely contribute to the success of these populations. Manipulative studies, including common garden and transplant experiments (Fox 1994; Belk 1995), should subsequently be performed to examine the extent to which the observed variation in life history traits is an outcome of phenotypic plasticity versus genetic differentiation (Belk 1995).

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Table 3-1. Physical and chemical characteristics of the four study lakes. Data are from the TROLS project core sampling program (see Prepas et al. 2001).

Lake	Latitude (°N)	Longitude (°W)	Surface area (ha)	Mean depth (m)	Max. depth (m)	Total phosphorus ($\mu g \cdot L^{-1}$)	Chlorophyll *a* ($\mu g \cdot L^{-1}$)
SCL100	55.13.00	111.65.67	18	3.5	7.6	24	11
SCL20	55.18.75	113.65.50	52	4.8	12.0	46	19
SCL200	55.10.50	113.73.42	109	0.6	2.1	58	12
SCL800	55.37.50	113.63.00	75	2.1	3.0	55	8.8

Table 3-2. Density, variation in density, and number of major winterkills of fathead minnows inhabiting the four study lakes from 1995-1999 (Chapter 2).

Lake	Mean density (#/m^3)	Range in density (#/m^3)	Coefficient of variation (%)	Number of large (> 47 %) declines over a 5 y period
SCL100	1.92	1.35-2.44	22.8	0
SCL20	3.75	2.22-5.37	33.6	1
SCL200	0.72	0.17-1.10	56.9	1
SCL800	0.14	0.02-0.37	93.5	2

Table 3-3. Body condition and gonadosomatic index (mean ± SE) of fathead minnows inhabiting the four study lakes from 1995-1998. M = male, F = female. Also reported are the results of statistical tests (ANOVA) comparing means among lakes; means with the same subscript did not differ ($P > 0.10$)

Lake	Body condition (slope of body weight vs. TL)		Gonadosomatic index	
	M	F	M	F
SCL100	2.27 ± 0.36	1.80 ± 0.38	$1.35 \pm 0.29_{a}$	$5.51 \pm 0.56_{a}$
SCL20	2.71 ± 0.35	2.13 ± 0.28	$1.26 \pm 0.21_{a}$	$6.56 \pm 0.57_{ac}$
SCL200	2.44 ± 0.23	2.11 ± 0.12	$2.44 \pm 0.44_{ab}$	$12.79 \pm 3.11_{bc}$
SCL800	2.55 ± 0.29	1.88 ± 0.14	$3.85 \pm 0.98_{b}$	$19.35 \pm 1.77_{b}$
$F_{(3,12)}$	0.47	0.48	6.16	14.45
P-value	$P > 0.1$	$P > 0.1$	$P < 0.01$	$P < 0.01$

Table 3-4. Indicators of reproductive activity (mean ± 1 SE; range in parentheses) for fathead minnow populations inhabiting the four study lakes from 1996-1998. CDD = cumulative degree days ≥15°C. Also reported are the results of statistical tests (ANOVA) comparing means among lakes.

Lake	Julian day at first reproduction	CDD at first reproduction (°d)	Julian day at peak reproduction	Duration of spawning season (d)
SCL100	158 ± 8	24.7 ± 0.9	174 ± 14	69 ± 4
	(142-169)	(22.9-26.2)	(146-193)	(63-76)
SCL20	155 ± 4	29.2 ± 11.4	168 ± 10	51 ± 9
	(146-161)	(9.8-49.4)	(162-188)	(34-56)
SCL200	147 ± 8	14.7 ± 2.3	160 ± 7	63 ± 8
	(132-157)	(10.1-17.1)	(146-168)	(55-79)
SCL800	142 ± 8	6.3 ± 3.5	161 ± 10	61 ± 10
	(132-157)	(1.8-13.3)	(146-180)	(49-80)
$F_{(3,8)}$	1.06	2.80	0.77	0.91
P-value	P > 0.1	P = 0.10	P > 0.1	P > 0.1

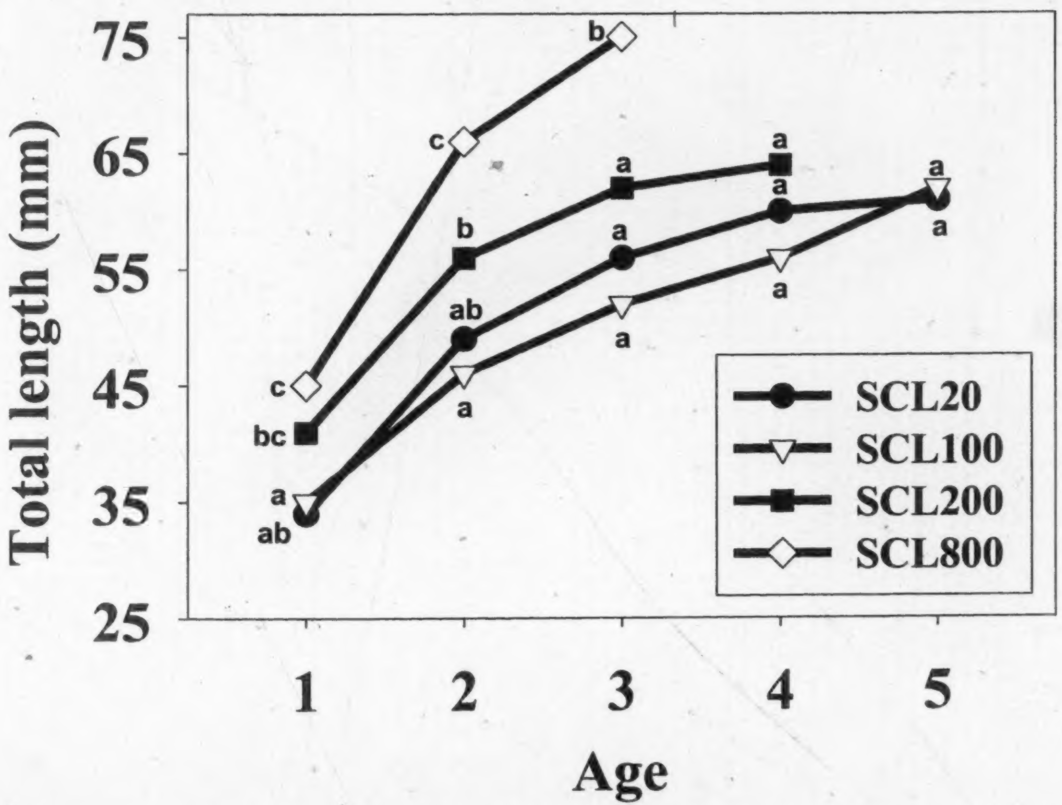

Figure 3-1 Back-calculated lengths (TL) at age for fathead minnows in the four study lakes. Lower case letters indicate significant differences ($P < 0.05$) for a given age across populations (Mann-Whitney U or Tukey's HSD).

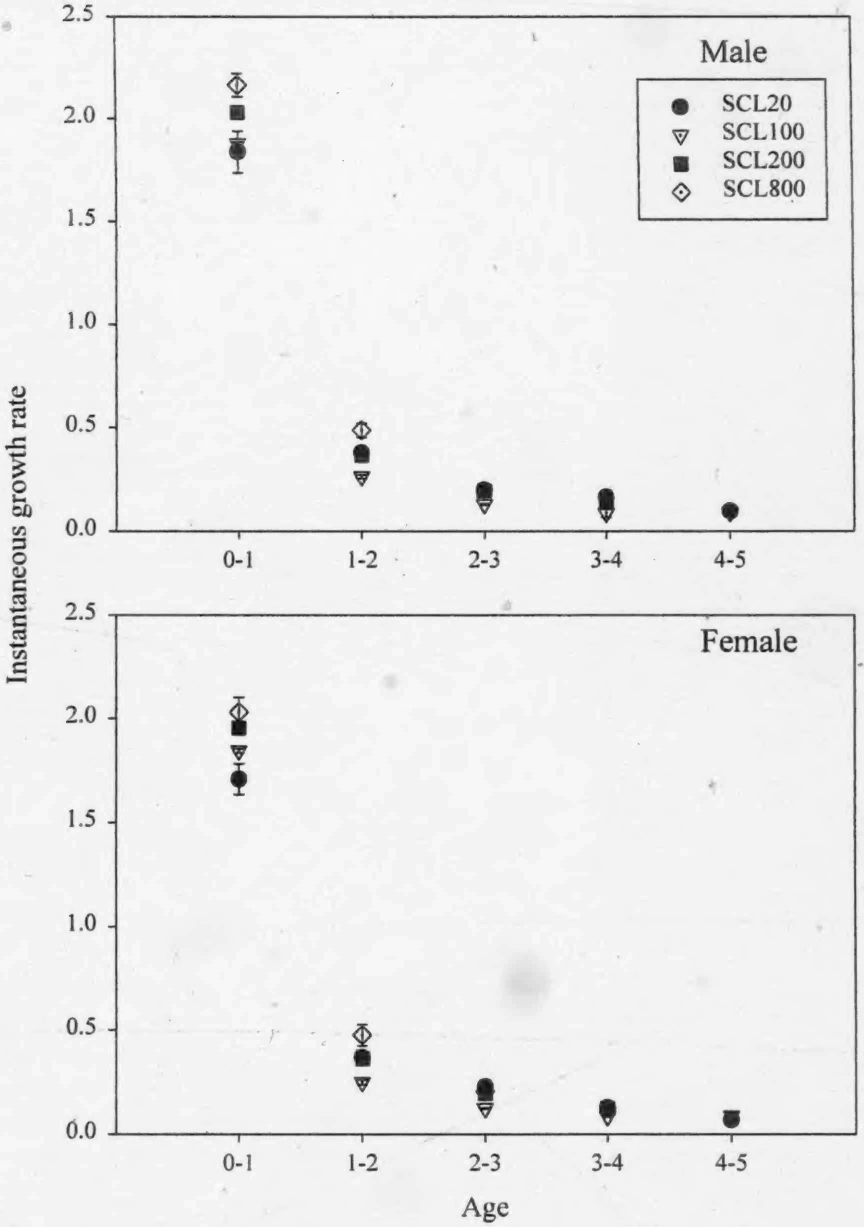

Figure 3-2 Age-specific instantaneous growth rates (± SE) for male (upper) and female (lower) fathead minnows in the four study lakes for fish collected from 1995-1998.

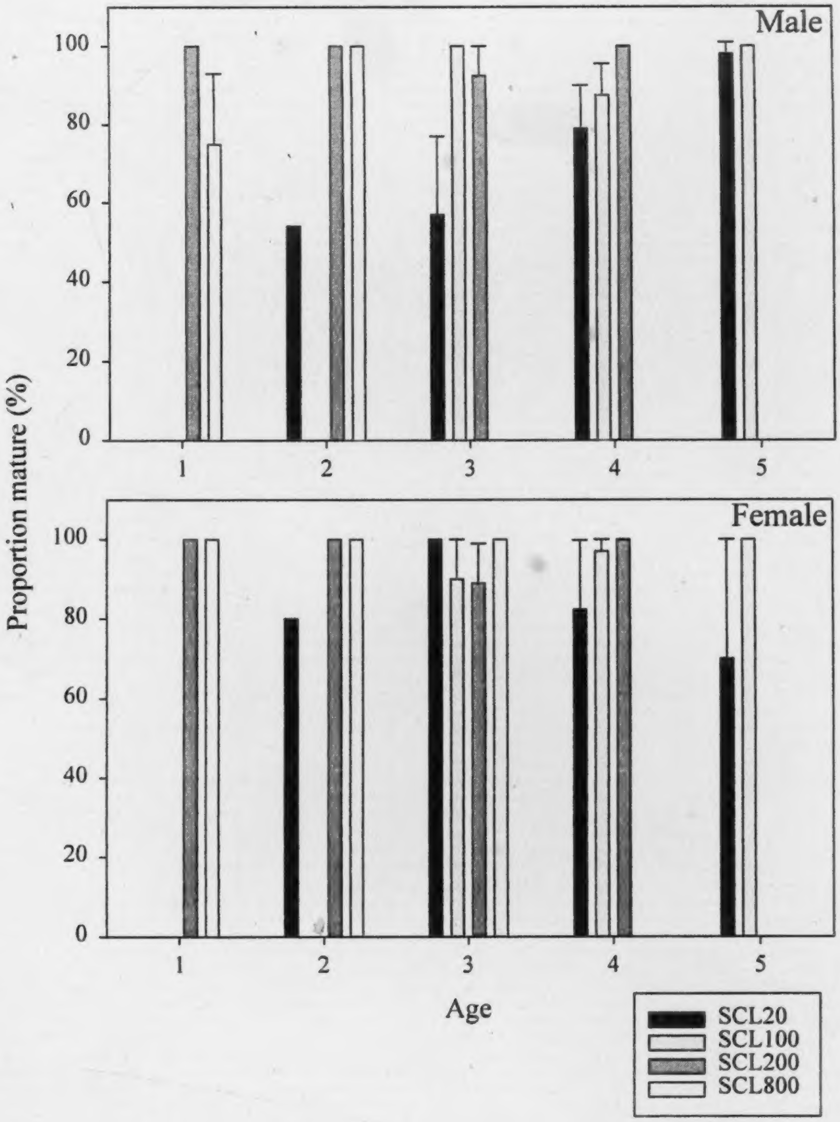

Figure 3-3 Mean proportion (± SE) mature versus age for male (upper) and female (lower) fathead minnows in the four study lakes collected from 1995 to 1998.

Chapter 4: Effects of social structure on reproductive activity in male fathead minnows, *Pimephales promelas*[2]

Introduction

To increase their fitness, individual organisms must adopt a strategy that effectively trades off energetic resources between reproduction versus somatic maintenance and growth (Stearns 1977; Kozlowski 1992). Traditionally, selection of a particular strategy within a population was thought to be frequency-dependent and based on an average fitness of alternative reproductive phenotypes for each sex (e.g., Gross 1991). However, the often extreme plasticity of reproductive phenotypes within sexes (Gross 1984; Starks and Reeve 1999) suggests that individuals make their life history trade off because of subtle differences in their immediate surroundings, and that those decisions may not have equal average fitness except at the switchpoint between alternative phenotypes (reviewed by Gross 1996). Consequently, ecologists have begun to consider the notion that alternative phenotypes result from individuals switching among tactics within a conditional, rather than an alternative, or mixed, strategy (Gross 1996).

Within a conditional strategy, switching between alternative reproductive tactics is commonly thought to be state-dependent (Gross 1996; McNamara and Houston 1996). Under this model, state is based on bioenergetics and an individual's physiological condition, with factors such as food supply (Kvarnemo 1997), nutrition (Tartar and Carey

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[2] A version of this chapter has been published. Danylchuk, A.J., and W.M. Tonn. 2001. Behavioral Ecology 12:482-489.

1995), and habitat availability (Williams et al. 1995) influencing when and how energy will be allocated to reproduction.

The timing of reproductive activity, in particular, is often size-dependent (Gauthreax 1978; Diana 1995), and nowhere is this more frequently documented than in fish (e.g., Foote 1988; Ridgway et al. 1991; Danylchuk and Fox 1994, 1996; Carscadden et al. 1997). Because of indeterminate growth, fish continue to increase in size after maturing and reproductively active individuals can therefore range considerably in body size. Consistent with models of state-dependent selection, size-dependent differences in the timing of reproduction in fishes are commonly explained by variation in physiological condition (e.g., Ridgway et al. 1991; Danylchuk and Fox 1994, 1996). Small fish should require more time to replenish over-winter energetic deficits than large fish because small fish have higher rates of energy use and lower available fat stores. Thus, small fish may be forced to delay seasonal timing of reproduction, resulting in asynchronous breeding activity between large and small individuals (Ridgway et al. 1991; Cargnelli and Gross 1997).

In contrast to state-dependence, more recent selection models based on a conditional strategy suggest that an individual's social status drives the decision between alternative tactics (see Gross 1996). In status-dependent selection, individuals use social interactions to evaluate their competitive ability in a population and the decision among alternative tactics is driven by the outcome of those interactions (Gross 1996).

There is ample evidence that social interactions can be a potent force in regulating reproduction for a wide variety of organisms (reviewed in Huntingford and Turner 1987). Individuals with higher social status can alter specific reproductive processes, such as ovulation in subordinate conspecifics by disrupting discrete neural and endocrine pathways (Bronson 1985). Dominant individuals can also influence more general reproductive functions of subordinates, such as their ability to hold a reproductive territory (Bronson 1985; Huntingford and Turner 1987; Stamps 1994).

Thus, an alternate explanation for variation in the timing of reproduction is that large individuals have a higher status in the population and socially interfere with the breeding opportunities of smaller individuals (Schultz and Warner 1989). Large individuals will often dominate when competing for reproductive sites or for access to mates (Munro 1990). Small individuals may thus evaluate their status from social encounters with larger, more dominant individuals and choose between alternative reproductive tactics accordingly. Consistent with this, the presence of large males has delayed testes development and timing of reproductive activity of small males in laboratory experiments (Borowsky 1973; Bushmann and Burns 1994).

Evidence for social control of reproductive activity also exists for natural populations of fish. The removal of large females from isolated coral heads advanced the ovarian development and reproductive activity of smaller females in the temperate wrasse, *Pseudolabrus celidotus* (Jones and Thompson 1980). As well, the number of adult males and the size of juveniles affected the proportion of maturing individuals in a population of variable platyfish (Borowsky 1978). More recently, Rodd et al. (1997) found that interactions with conspecifics influenced development and size at maturity of male guppies, *Poecilia reticulata*, which, in turn, may have influenced reproductive status.

Although this evidence indicates that social status can influence the timing of reproduction in individual fish, few studies have examined the effects of social control of reproduction at the population-level. Anecdotal evidence suggests that social status plays a role in the timing or occurrence of reproduction of male fathead minnows (*Pimephales promelas*) (P. V. Hodson, personal communication; W. M. Tonn, personal observations).

As part of my investigations into the factors influencing the population structure and life history characteristics of fathead minnows inhabiting boreal lakes, I conducted two field experiments in small ponds to determine whether social environment modulates the timing of reproductive activity in male fatheads and, if so, how this might influence population growth or regulation. I predicted that if the decision to reproduce is state-dependent, differences in the social environment should have little impact on the seasonal timing of reproduction in male fathead minnows. If, however, the social environment influences the decision to reproduce, individuals of lower status should accelerate reproduction when dominant conspecifics are absent.

Methods

I conducted an enclosure experiment in a small pond at the Meanook Biological Research Station (MBRS), Alberta, Canada, to determine whether social environment affects the seasonal timing of reproductive activity in small male fatheads. Based on these results, I conducted a second experiment in larger dugout ponds to assess the effects of social structure on reproduction at the population-level.

Enclosure experiment

Small males (50-58 mm TL) were stocked in enclosures under three different social regimes: (a) 15 small males and 5 large (63-70 mm TL) males (SM+LM), (b) 15 small males and 5 large males, with large males removed after approximately three weeks (SM+LM(R)), and (c) 20 small males without large males (SM). Five mature females (+F) were also added to each enclosure to facilitate reproduction. I predicted that if large male fatheads socially interfere with the reproductive activity of smaller males, then some small males in the SM+F social group should become reproductively active earlier in the season than small males in the SM+LM+F or SM+LM(R)+F social groups. Moreover, if large males are socially dominant, then reproductive activity of small males in the SM+LM(R)+F social group should increase once the large males are removed relative to males in the SM+LM+F social group.

Five blocks of three enclosures each were built using impermeable polyethylene curtains, supported by wooden frames driven into the substrate of the pond. Sand and rocks secured the bottom of enclosures to the substrate. Enclosures were 3 m x 2 m and I maintained pond water levels within the enclosures at approximately 1 m. As a result, fish densities within the enclosures (4 fish•m^{-3}) approximated densities of natural populations within the region (Chapter 2). Each social group was randomly allocated to one enclosure within each block.

During the breeding season, reproductively active male fathead minnows establish territories around the underside of structures, such as snags, lily pads (Wynne-Edwards 1932; Andrews and Flickinger 1969), and introduced nesting substrates (Benoit and Carlson 1977). From these territories, males actively court females and, if courtship is successful, females will deposit a batch of eggs on the underside of the defended structure via an ovipositor. As such, I added floating fence boards anchored to bricks to serve as spawning substrate. Seven nestboards were deployed in each enclosure (one large (100 x 4.5 cm), three medium (35 x 4.5 cm), and three small (25 x 4.5 cm)) and the placement of nestboards was identical for all treatments.

In early June, just prior to the onset of reproduction, I collected fatheads from a SCL20, 70 km north of MBRS. Fish were transported to MBRS and allowed to acclimate for 4 d in large outdoor tanks. During this period I fed the fish freeze-dried *Daphnia* and flaked food.

Following the acclimation period, fish were measured (TL, mm), weighed (wet, 0.01 g) and sorted according to gender based on the presence of secondary sexual characteristics. I selected fish so as to minimize the range in total length within each gender or size group. The mean size of individuals in each group did not differ among social treatments (ANOVAs, P>0.1).

I assigned each male and female a score based on the degree to which secondary sexual characteristics were developed. During the breeding season, fatheads are sexually dimorphic. Reproductively active males develop rows of nuptial tubercles on the front of the head and lower jaw, a thick, spongy dorsal pad anterior of the dorsal fin for cleaning eggs, and dark body coloration broken by two golden vertical bands (Markus 1934; Flickinger 1969). Females develop an extrusion of the gonadal papilla (ovipositor) and a distended abdomen when gravid (Flickinger 1969). Juveniles lack all of these characteristics, although I can use subtle differences in head, anal fin, and gonadal pore morphology to help identify gender prior to the onset of maturity; immature males have a broader, rounder head and a larger anal fin than females. As well, although quite small, the ovipositor appears well before females begin to mature and can be used as a final trait to differentiate gender in immature fatheads (Flickinger 1969; personal observations).

The development of the secondary sexual characteristics is positively correlated with gonadal development; Smith (1978) found that peak tubercle and dorsal pad development in males coincided with the final stages of spermatogonia development and peaks in the gonadosomatic index. Therefore, secondary sexual characteristics not only provide a means of differentiating gender, but the degree to which they are developed is a good indicator of reproductive condition.

I scored males according to the development of tubercles and dorsal pad (maximum possible score = 6) and females according to the development of the ovipositor and the degree to which the abdomen was distended (maximum = 5; Table 4-1). Large males used in the experiment had secondary sexual characteristic scores of 5-6; all experimental females had scores of 4-5. Small males were all reproductively undeveloped and had a score of zero; I used the morphology of the head, gonadopore, and anal fin to sex fish in this size category (see below for validation procedure).

To determine the repeatability of my assignments of secondary sexual characteristic scores, I placed 20 fish at various stages of development in individual 1-L beakers and scored them according to external reproductive traits. I wrote the score on a label, adhered it to the bottom of the beaker, and after 1 hr randomly rearranged the beakers and re-evaluated the secondary sexual characteristics of the fish. I repeated this process three times. I then coded the scores of individual fish as change or no change between trials and examined the consistency of scoring using Cochran's Q-test for repeated measures of dichotomous variables (Zar 1996). In addition, I compared the mean scores among these trials with a Kruskal-Wallis test to determine if changes in scores resulted in significantly different mean scores between trials.

To keep track of fish throughout the enclosure experiment, I batch-marked small males, large males, and females with distinct colors of non-toxic acrylic paint, which was subcutaneously injected on either side of the body just posterior to the base of the dorsal fin using a 1 cc tuberculin syringe with 23 3/4 G needle (Unger 1983). I monitored marked fish for 24 hours prior to stocking to determine if there were any adverse effects of marking. If a fish was considered distressed (6 of 375 marked fish), it was replaced with an individual of similar size, gender, and secondary sexual characteristic score.

I stocked fish into enclosures on 14 June 1996. To examine the reproductive condition of individuals in each social group, I collected a subsample of fish with minnow traps approximately every ten days. I measured, weighed, and scored individuals in each gender group for secondary sexual characteristics, then returned them to their respective enclosure. Concurrently, I checked nestboards for eggs.

I added Nutrafin® flaked food to each enclosure at 5% body mass per day throughout the experiment to ensure survival and reduce or eliminate effects of intraspecific competition for food resources. Feeding also helped control effects of density on food intake once adult males were removed from the SM+LM(R)+F social group.

Pond experiment

I divided three dugout ponds (30 m x 12 m) in half with an impermeable polyethylene curtain secured firmly into the substrate. I collected fatheads from a small lake 35 km southeast of MBRS, and measured, weighed, and sorted individuals by gender and size. For each gender group, I scored individuals according to their secondary sexual characteristics and batch-marked fish with acrylic paint for future identification.

On 3 June 1997, I stocked SM+LM+F and SM+F social groups in either half of each pond using the same density (4 fish•m^{-3}) and ratios among small and large males and females as in the enclosure experiment. Because pond halves differed somewhat in size, total numbers stocked varied between 291 and 385 fish. To provide spawning substrate, I placed seventeen nestboards in each pond half. I maintained the water level in each pond at 1 m throughout the experiment and placed a temperature data logger in ca. 30 cm of water in each pond half, recording water temperature hourly throughout the experiment. The thermal regime of each pond half was characterized by calculating mean monthly cumulative degree-days (≥15°C) for each treatment.

To assess the reproductive condition of individuals during the experiment, I made weekly collections of ca. 100 fish from each pond half using unbaited minnow traps. Pond halves were processed in random order and the scorer of reproductive condition was ignorant of the treatment group of the fish. I sorted fish by their acrylic mark for gender and size-class, measured, weighed, and scored individuals according to their secondary sexual characteristics, and then returned them to their respective pond half. To validate my sexing criteria, I determined the proportion of fish initially classified and marked as reproductively inactive males that later developed into clearly distinguishable males (based on secondary sexual characteristics).

To examine reproductive patterns, I checked nestboards weekly for the presence of eggs. When conditions permitted (e.g., low turbidity, bright sunshine), I conducted timed snorkeling surveys to classify the individuals holding nesting territories as either a large or small male. I defined a male as holding a nesting territory if he was observed aggressively defending the underside of a nestboard, regardless of whether eggs were present.

To determine whether small males in the absence of large males were able to produce similar numbers and sizes of young as large males, and contribute equally to recruitment of young fish into the population, I collected young-of-the-year (YOY) towards the end of the growing season. I made five 5-m tows with a net (30 cm diam., 2 mm mesh) and three 5-m passes with a portable electroshocker. I euthanized YOY with tricaine methanesulfonate (MS 222), preserved them in 80 % ethanol, and later enumerated and measured them (standard length, SL) to the nearest 0.1 mm.

Data analysis

In all cases, I determined mean values from replicates of each social group. Differences among social groups were considered marginally significant if $0.1 \geq P > 0.05$ and significant if $P \leq 0.05$. To test my predictions, I used parametric tests (Student's t-test, one-way ANOVA) for continuous data and nonparametric statistics (Kruskal-Wallis, Mann-Whitney U-test, Kolmogorov-Smirnov two-sample test) for categorical data. All statistical analyses were performed using Systat version 5.2 for the Macintosh.

Results

The score repeatability test confirmed that my criteria for scoring secondary sexual characteristics were stable and repeatable. Among the three trials, repeated scoring did not differ (Cochran's Q-test, Q=0.67, P>0.05) and the changes that did occur (20% of the fish) did not alter mean secondary sexual characteristics scores among trials (Kruskal-Wallis, H=0.360, P=0.835).

Similarly, my criteria used to identify gender of reproductively inactive fatheads was reliable. Of the fish collected for the seven sampling periods in June and July of the pond experiment, less than 12% of those marked as small males developed into females (number of fish marked as small males examined per assessment period, 52-139; mean proportion of misclassified small males for each pond half, 8.0-11.2%; standard deviations, 3.1-6.8%).

Enclosure experiment

Small males in the SM+F social group developed secondary sexual characteristics more rapidly and to a greater extent than small males in either the SM+LM+F or the SM+LM(R)+F social groups (Figure 4-1a). Within the first two weeks, mean secondary sexual characteristic score of small males was two units higher in the former social group than the latter two groups (Kruskal-Wallis, H=4.57, P=0.10). Although scores of individuals varied considerably within the SM+F group and the distributions of scores among treatments was only marginally significant (K-S test, P<0.1), 58 % of small males in the group had scores of 5-6, compared with a combined total of 28 % for the other two social groups.

The proportion of small males expressing fully developed secondary sexual characteristics (scores of 5-6) in the SM+LM+F social group peaked in early July at 22 %, declining to 10 % 10 d later. Although initially similar to the SM+LM+F group, the proportion of small males expressing fully developed secondary sexual characteristic scores in the SM+LM(R)+F social group continued to increase, from 30% to 50 %, after removal of the large males. By mid-July, mean scores of small males in the SM+LM(R)+F and SM+F social groups were equal, and both were greater than those in SM+LM+F social group (Figure 4-1a).

Nesting activity and spawning began within 2 d of each other in all treatments (Figure 4-2a). The number of active nests did not differ among social groups for all assessment periods (one-way ANOVA, P>0.1). Nevertheless, small males held territories only in the SM+F social group or once large males were removed from the SM+LM(R)+F social group (personal observations). Peak nesting activity occurred at the same time in all social groups, but nesting activity persisted longer in the SM+LM(R)+F and SM+F social groups than the SM+LM+F social group.

Despite these differences in development of secondary sexual characteristics and spawning activity among treatments, growth of small males was similar among the three social groups (Figure 4-3a; one-way ANOVAs on lengths, P>0.1). Furthermore, fish condition measured as Fulton's condition factor (weight/length^{-3} x 100; Weatherley 1972) did not differ among treatments during any assessment period (one-way ANOVA, P>0.1), and temporal patterns of condition were similar for small males in all social groups.

Pond experiment

Small males in the SM+F social group developed secondary sexual characteristics more rapidly than small males in SM+LM+F social group, attaining significantly higher scores during the first three assessment periods (Figure 4-1b; Mann-Whitney U-test, $P<0.05$). The distribution of small males at each secondary sexual characteristic score also differed between treatments during this period (K-S test; $P<0.05$), with over 62% of small males in the SM+F group having scores of 5-6, compared to 33 % for the SM+LM+F social group. Mean secondary sexual characteristics scores of small males in the SM+LM+F social group eventually equaled that of small males in the SM+F social group, but this peak occurred approximately 2 wk later in the season.

In both social groups, spawning began soon after fish were stocked and two distinct peaks in activity occurred, one in mid-June, the other in mid-July (Figure 4-2b). The mean number of nests observed during the first peak in spawning activity was similar for both social groups, but was higher for the SM+LM+F social group during the second peak than for the SM+F treatment. However, differences in mean number of nests between social groups were not significant for any assessment period (Student's t-test, $P>0.1$).

Thermal regimes at the end of each month during the experiment were similar for both social groups (Student's t-test; June, $P=0.29$; July, $P=0.30$; August, $P=0.31$), although mean monthly cumulative degree-days ≥15°C was 11-17% lower in the SM+F ponds than in the SM+LM+F ponds. Nevertheless, there were no apparent trends between thermal regime and the initiation and intensity of spawning activity for either social group.

Snorkeling surveys were conducted four times throughout the pond experiment. During each survey, the mean number of males holding territories was similar for the two social groups (Table 4-2; Mann-Whitney U-test, $P>0.05$). However, during the June survey, only large males held nesting territories and spawned in the SM+LM+F social group. These large males aggressively defended their nesting territories associated with nestboards, successfully deterring small males from establishing territories. This happened regardless of whether a large male was holding a territory on that particular board or on an adjacent board. By mid-July, some small males began to hold nesting territories in the presence of large males; however, the number of small males doing so was relatively low (Table 4-2).

The average length of small males increased by > 22% throughout the course of the experiment and did not differ between social groups when the experiment ended in late August (Figure 4-3b; Student's t-test, $P>0.1$). Between late June and mid-July, however, small males in the SM+LM+F social group were larger than small males in SM+F social group (Student's t-test, period three, $P\leq0.1$, period five $P\leq0.05$). Despite these differences, condition of fish was similar between treatments during each assessment period (Student's t-test, $P>0.1$).

At the end of the summer (25 August), the number of YOY produced by each social group was similar (Student's t-test, $P>0.5$). Moreover, the size of YOY ranged between 7 and 31 mm standard length (SL) for both social groups (Figure 4-4) and mean size did not differ (Student's t-test, $P>0.1$). However, the size distributions of the YOY (measured by a randomly selected subsample of 75 YOY from each replicate pond for each treatment) differed between treatments (K-S test; $P<0.05$). In the SM+LM+F social group, the distribution was bimodal (ca. 11 and 18 mm SL), with similar numbers in each mode, whereas the size distribution of YOY produced by the SM+F social group was unimodal (10 mm) with relatively few individuals >15 mm.

Discussion

My study indicates that social environment can modulate the seasonal timing of maturation and reproduction in male fathead minnows. In both the enclosure and pond experiments, the presence of large males inhibited or delayed the reproductive activity of small, initially immature males. Indeed, small males held nesting territories only after large males were removed from the population (enclosure experiment), or when nesting activity of large males began to drop off (pond experiment).

If small males postponed reproduction due to their physiological state, as is frequently postulated (e.g., Cargnelli and Gross 1997), small males in better condition, regardless of their social group, should have initiated reproductive activity earlier. In contrast to this prediction, however, small males that initiated reproduction were neither larger nor in better condition than reproductively inhibited small males. In fact, inhibited males in the pond experiment displayed somewhat faster growth than small males that occurred without large males, particularly during peak weeks of nesting by large males and by the latter group of small males. Thus, it appears that social status influenced the bioenergetic trade-off decision of small males, consistent with the model of status-dependent selection (Gross 1996).

In status-dependent selection, individuals select between alternative phenotypic traits based on their status relative to that of other individuals in the population (Gross

1996; Pusey and Packer 1997). For example, the choice between holding a reproductive territory or wandering among territories in male wood-carder bees, *Anthidium manicatum*, depended on relative, not absolute, body size (Starks and Reeves 1999). Thus, when large territory holders were removed, they were replaced by small males that previously employed the wandering tactic (Starks and Reeves 1999). Although I did not follow individuals in my experiments, the ability of small males to quickly become territory holders once I removed large males from the SM+LM(R)+F social group (enclosure experiment) shows that small males have the capacity to switch between alternative tactics in response to changes in their social status.

Since interactions among conspecifics affect individual status, the expression of alternative phenotypes should be sensitive to ecological and demographic events that influence those interactions (Gross 1996). For example, north-temperate fishes inhabiting small productive lakes and ponds are often subjected to low winter oxygen conditions causing over-winter mortality, or winterkill, that tends to affect larger individuals disproportionately (Casselman and Harvey 1975; Barica and Mathias 1979; Robinson and Tonn 1989). Although the fathead minnow is tolerant of low winter oxygen conditions, the demographic characteristics (size structure and abundance) of fathead populations in northern lakes and ponds are influenced by the severity of oxygen depletion, which can vary dramatically from year to year (Chapter 2). As such, the relative size-dependent status of individuals likely varies from year to year in lakes that are prone to winter oxygen depletion, and is less variable in lakes that do not winterkill. Thus, it is reasonable to hypothesize that phenotypic diversity is greater in lakes that are prone to winterkill, because of selective pressures that result from social interactions and the drive to increase fitness when social environments change rapidly.

In north-temperate fishes, parents may try to maximize their fitness by producing young earlier in the breeding season. Spawning early in the season could increase the probability of the recruitment of young into the future population (reviewed in Daan and Tinbergen 1997) because over-winter survival of small individuals is highly dependent on prior accumulation of sufficient energy reserves (Keast 1968; Oliver et al. 1979; Post and Evans 1989; Shuter and Post 1990). In my pond experiment, the numbers of young produced in the two treatments (SM+F versus SM+LM+F) were similar, although the size distribution of young produced in the SM+F social group was skewed towards small body sizes at the end of the growing season. Because the intensity of competition for food in fathead minnows is related to their similarity in body size (Vandenbos 1996), competition on YOY may have been stronger in the SM+F social group than in the SM+LM+F group, especially since the number of potential SM competitors in the former group was greater than in the latter at the end of the growing season (Danylchuk and Tonn, unpublished data). Alternatively, the difference in size distributions between treatments may be the outcome of offspring expressing inherited paternal traits resulting from the indirect genetic effects of 'interacting phenotypes' (sensu Moore et al. 1997) and the structure of the social environment. Regardless of the underlying mechanism, the potential reduced fitness of the uninhibited small males in the pond experiment is consistent with the model of status-dependent selection under a conditional strategy, which predicts unequal average fitness of alternative phenotypes (Gross 1996).

Phenotypic diversity observed within and among fathead minnow populations inhabiting boreal lakes is high (Chapter 3), and my results suggest that the structure of the social environment may account for much of this variability. At the population level I found that social environment affected the seasonal timing of reproduction in males and the size distribution of their young, which may, in turn, influence key processes such as recruitment and population growth. However, to refine these predictions, a better understanding of the mechanisms through which social interactions affect population-level processes is needed. Social structure within populations is both an environment and an evolving trait and, as a result, the potential population-level consequences of this structure are numerous.

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Table 4-1. Scoring criteria for male and female secondary sexual characteristics.

	Males		Females	
Score	Tubercles[a]	Dorsal pad	Ovipositor	Abdominal Distention
0	no visible sign of tubercles	no visible sign of dorsal pad	no visible sign of ovipositor	fish streamline, no noticeable lateral distention
1	tubercles visible as white disks, not protruding above body surface	epidermis between head and dorsal fin becoming 'spongy' along medial ridge	ovipositor visible as small protrusion at gonadopore; soft and flaccid	abdomen becoming somewhat distended laterally (when viewed dorsally)
2	tubercles protruding above body surface but not sharp	dorsal pad increasing in width; thickening but only a slight nape behind head	ovipositor becoming rigid and increasing in length	abdomen extremely distended; streamline form greatly compromised
3	tubercles prominent and sharp	dorsal pad wide and thick, forming a sharp nape posterior to head when viewed laterally	ovipositor large and very rigid	

[a] modified from Smith (1978)

Table 4-2. Mean number of large and small males observed holding nesting territories in each treatment (social group) during snorkeling surveys in the pond experiment. Individuals that could not be identified as large or small males (using their paint mark) were classified as unknown territory holders.

Survey date	Treatment	mean # of large male territory holders	mean # of small male territory holders	mean # of unknown territory holders
11 June	SM+LM+F	15	0	0
	SM+F	-	12	0
14 July	SM+LM+F	14	1	3
	SM+F	-	17	0
23 July	SM+LM+F	7	2	1
	SM+F	-	9	0
4 August	SM+LM+F	0	0	0
	SM+F	-	0	0

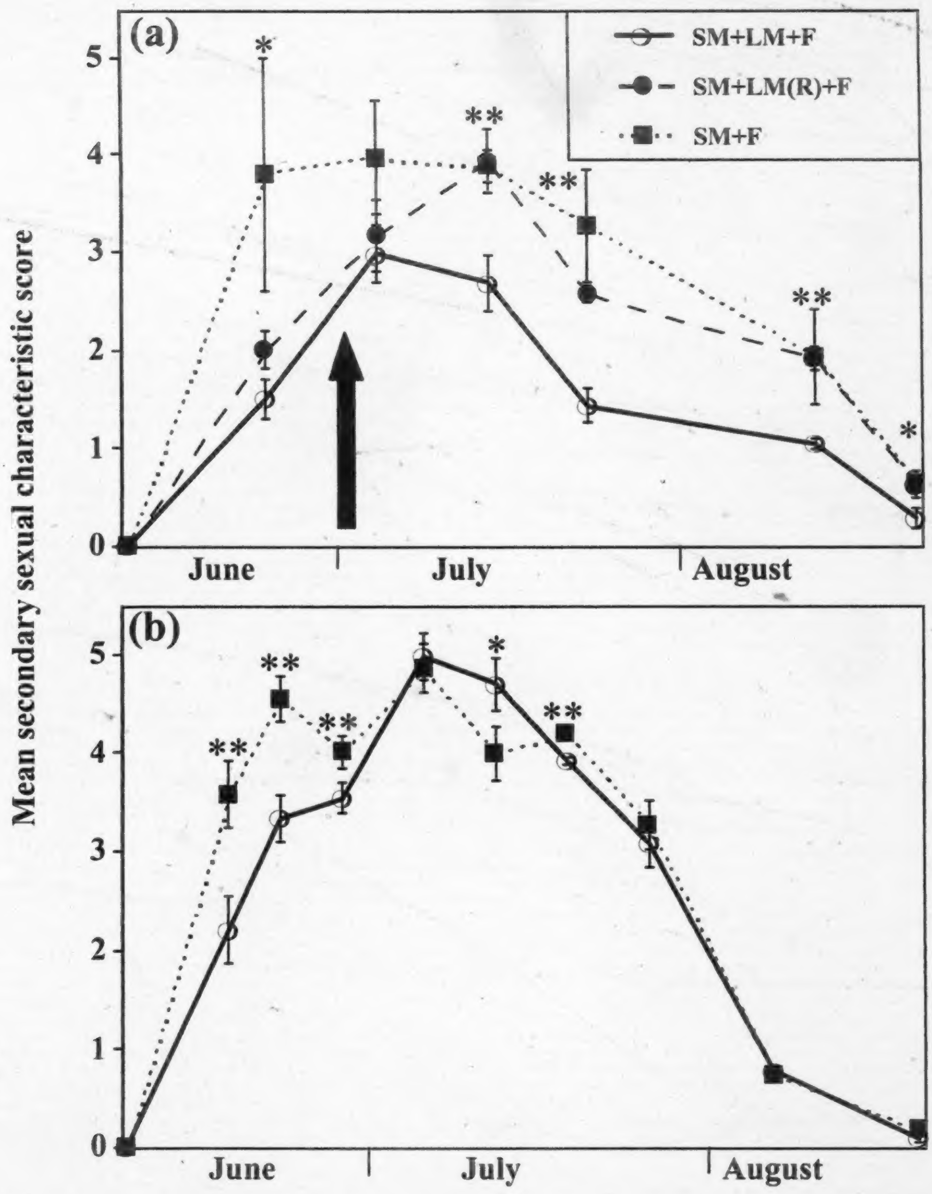

Figure 4-1. Mean secondary sexual characteristic score (± 1 SE) of small males for each social group sampled during the enclosure (a) and pond (b) experiments. The arrow in (a) indicates when large males were removed from the SM+LM(R)+F social group. **P*≤0.1 and ***P*≤0.05 for differences among treatments.

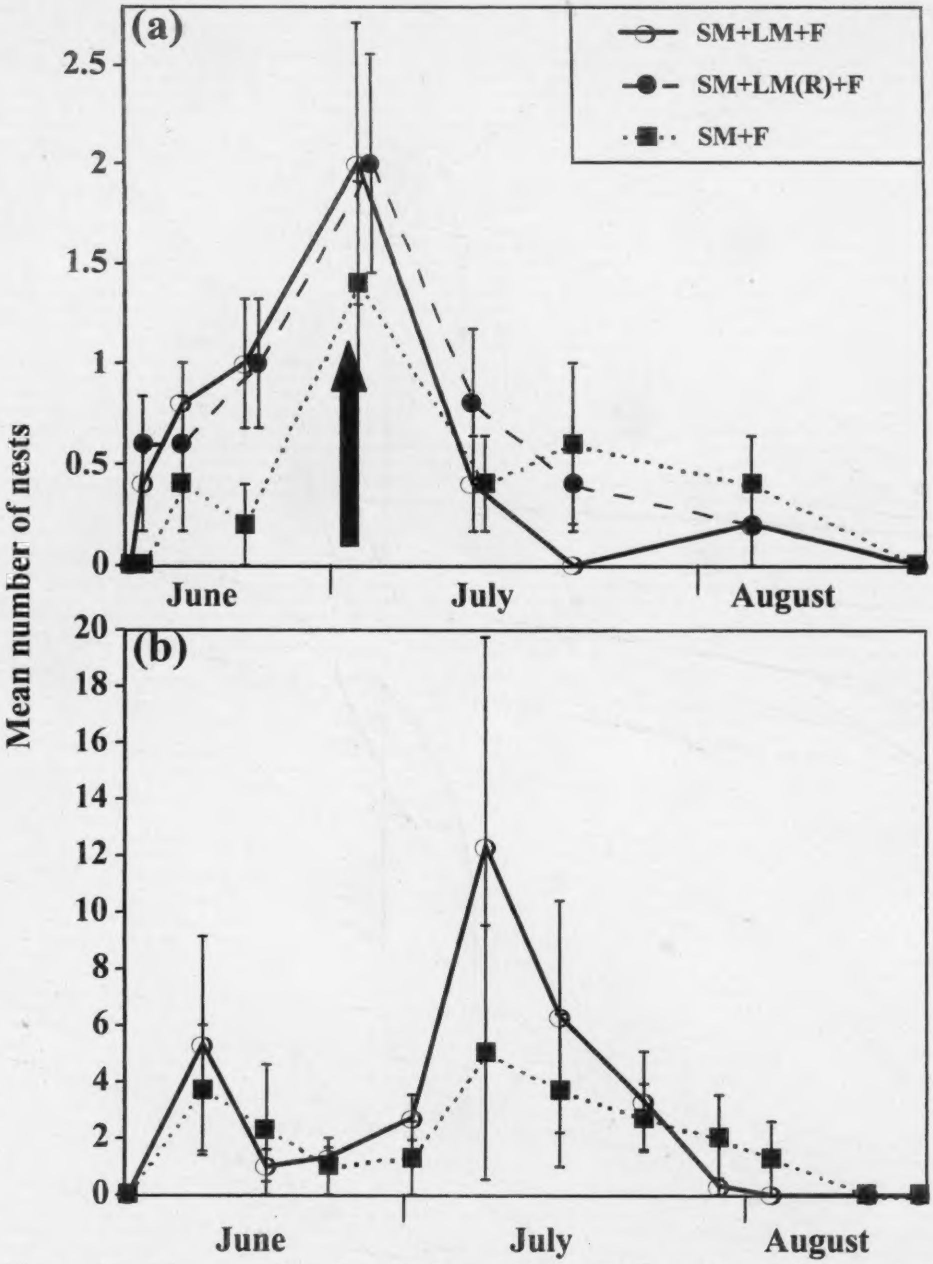

Figure 4-2. Mean number of nests observed (± 1 SE) for each social group during the enclosure (a) and pond (b) experiments. The arrow in (a) indicates when large males were removed from the SM+LM(R)+F social group.

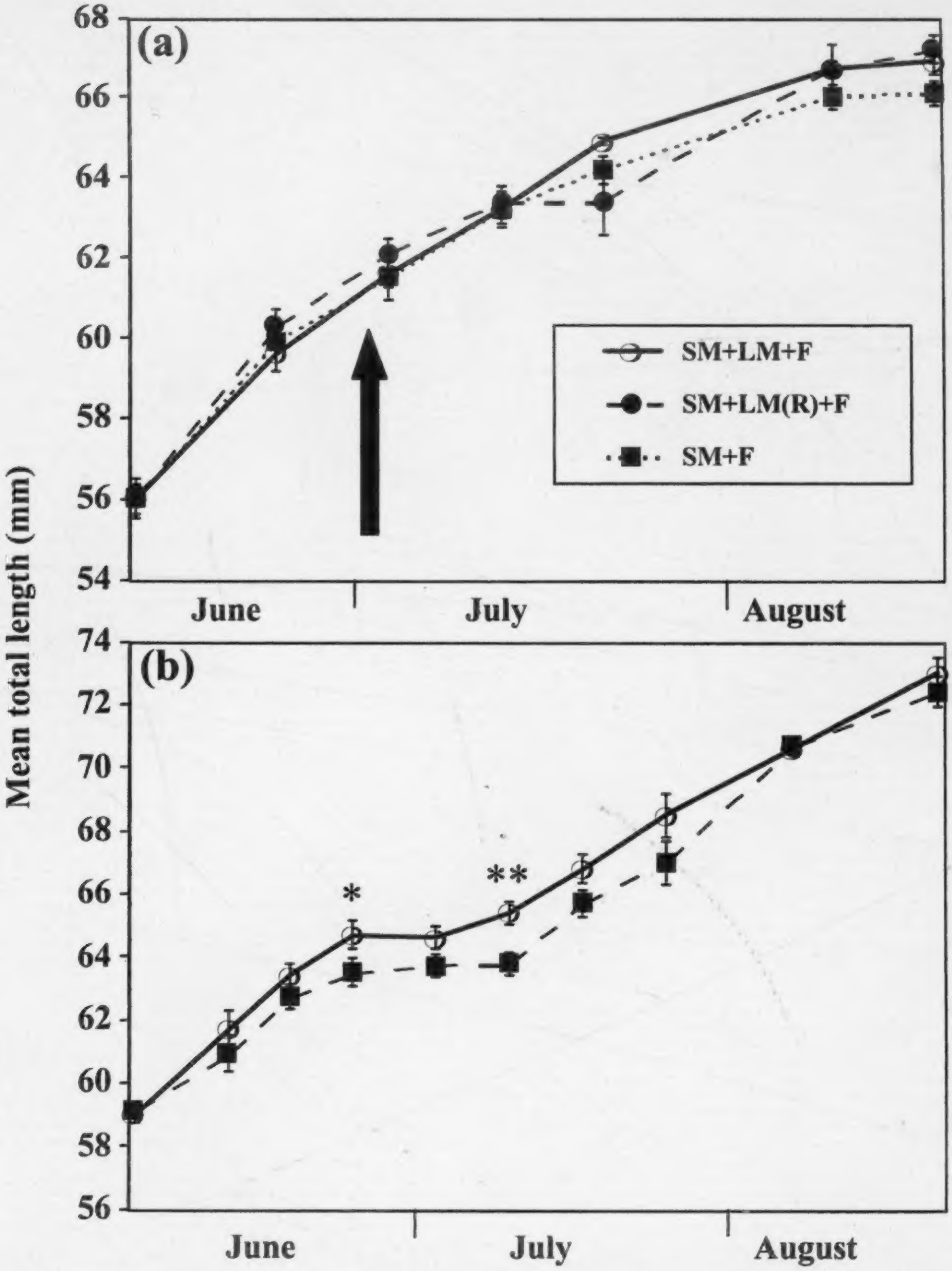

Figure 4-3. Mean total length (± 1 SE) of small males for each social during the enclosure (a) and pond (b) experiments. The arrow in (a) indicates when large males were removed from the SM+LM(R)+F social group. **P*≤0.1 and ***P*≤0.05.

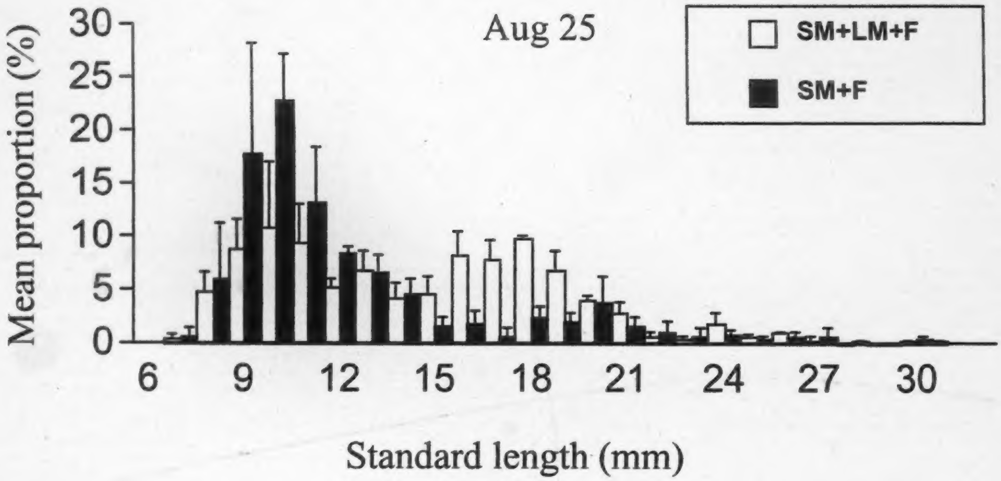

Figure 4-4. Length-frequency distributions (+ 1 SE) of young-of-the-year fathead minnows collected on 25 August from the SM+LM+F and SM+F social groups during the pond experiment. The proportion of fish in each size category was determined for each replicate (sample sizes ranging from 93 to 277), from which means were derived for each social group (n=3 for each group).

Chapter 5: Relationship between catch-per-unit-effort and estimates of absolute abundance in fathead minnows: a useful tool for monitoring small-bodied fishes in boreal lakes

Introduction

Estimating abundance is essential for studying the ecology and demographics of fish populations (Hilborn and Walters 1992; Krebs 1994). Obtaining reliable abundance estimates is generally the first step to understanding the responses of populations to ecological or environmental disturbances that influence population growth through their affects on mortality and recruitment (Hilborn and Walters 1992). In addition, estimating abundance is crucial for sound management of commercial and recreational fisheries (Hilborn and Walters 1992).

Ideally, accurate and precise estimates of abundance are obtained by direct enumeration; however, this method can be expensive, labor intensive, and is not practical for most fish species (Hilborn and Walters 1992). Alternatively, indirect methods are often used to generate estimates of abundance, and such methods are usually less costly, require less effort, and are able to generate relative estimates with very respectable levels of error (Hilborn and Walters 1992). One such method is mark-recapture surveys from which estimates of absolute abundances are generated (Everhart and Youngs 1981; Krebs 1994). Although appealing, mark-recapture surveys can be tedious if large numbers of fish need to be marked to achieve reasonable precision, especially when abundance is high (Robson and Regier 1964). As such, mark-recapture surveys are often impractical for fisheries surveys in remote locations, simply due to associated logistical constraints (Gresswell et al. 1997).

To minimize time and logistical constraints, catch-per-unit-effort (CPUE) can be used to generate in an index of abundance rather than a true numerical estimate of fish within a population. However, if CPUE is to be used as a true surrogate of population size, the relationship between CPUE and absolute abundance must either be quantified directly or assumed (Harley et al. 2001). In addition, CPUE cannot be easily transformed into other useful population metrics, such as density or biomass, unless the relationship between relative and absolute abundance is established.

Small-bodied fishes are often quite abundant in northern boreal lakes because of their ability to contend with overwinter hypoxia, and subsequently thrive in the absence of less-tolerant piscivores (Magnuson et al. 1985; Robinson and Tonn 1989; Tonn et al. 1995; Chapter 2). However, in spite of their tolerance to low oxygen, the abundance of small-bodied fishes can vary dramatically among lakes and years because of variation in climate and population-level differences in susceptibility to winterkill (Chapter 2); this variation can subsequently contribute to other patterns in northern aquatic ecosystems (e.g., Zimmer et al. 2001). Variability in northern aquatic ecosystems may also be affected by human disturbances, which are increasing in frequency and severity (Schindler 2001). For instance, climate warming, forest harvesting, and agriculture can all cause an increase in nutrient loading to lakes (Schindler et al. 1990; Cooke and Prepas 1998; Carignan et al. 2000; Schindler 2001), that could, in turn, increase winter oxygen depletion and augment the natural incidence of winterkill. However, quantifying the effects of such human activities on small-bodied fish populations requires reliable estimates of abundance at spatial and temporal scales sufficient to filter out the effects of natural disturbance. Unfortunately, tens of thousands of fish often need to be marked in order to achieve reasonable recapture rates (Danylchuk and Tonn, unpublished data), thus a rapid, less labor intensive, yet reliable way of estimating absolute abundance could allow the spatial and temporal dimensions of studies on small-bodied fishes to increase, especially in remote areas.

As part of my investigations into the factors influencing population structure and life history characteristics of fathead minnows (*Pimephales promelas*) inhabiting remote boreal Alberta lakes, I conducted mark-recapture surveys of four populations over a 5-year period (Chapter 2). Since I collected catch data for individual traps during these surveys, I was able to examine whether CPUE could provide results similar to those generated by mark-recapture. In addition, I was able to generate a simple model between relative and absolute population estimates, and test the model with data from a fifth, independent population to determine whether CPUE can be reliably used to generate absolute abundance estimates.

Methods

Population estimates

The four fathead minnow populations inhabited lakes within 30 km of each other, in a roadless area about 200 km north of Edmonton, Alberta. The study lakes were in the South Calling Lake (SCL) study region of the Terrestrial and Riparian Organisms Lakes and Streams (TROLS) project (see Prepas et al. 2001), and were designated as SCL20, SCL100, SCL200, and SCL800. The fifth population used to test my model also inhabited a lake in the SCL study region (TROLS11), ca. 1.5 km from SCL100.

I conducted annual multiple-census mark-recapture surveys for each of the four study populations from 1995-1999 (Chapter 2); the population in TROLS11 was surveyed in 1998. Following these surveys, abundance was estimated using the Schnabel method, which essentially derives a weighted average estimate of repeated Petersen model estimates for closed populations (Ricker 1975). Assumptions associated with this method include equal mortality and vulnerability of capture for marked and unmarked fish and for different segments of the population, no loss of marks and marks remaining recognizable throughout the survey period, distribution of marked and unmarked fish is independent and random, and recruitment, immigration, and emigration are negligible (Ricker 1975).

I carried out surveys over a 7-9 d period before the onset of reproductive activity. The relatively short duration of the surveys (and relative isolation of the lakes) eliminate recruitment, immigration or emigration, and reduce the probability of unequal mortality among marked and unmarked fish (Gresswell et al. 1997). In addition, conducting surveys prior to the onset of reproduction should reduce variability in the likelihood of capture that might result from differences in reproductive behavior and distribution. To further avoid bias caused by gender-specific differences, I marked fish differentially based on gender and maturity, and generated separate abundance estimates for male, female, and juvenile fatheads. Fish were marked with small angular clips of the caudal or anal fin using sharp dissection scissors. Marks were highly discernible and regrowth was unlikely to occur because of the short duration of the surveys. Fathead minnows are also quite hardy, being cultured extensively for the commercial baitfish industry (Etnier and Starnes 1993) and for toxicological research (e.g., Brazner and Kline 1990), and small fin clips likely had little affect on behavior or survival.

Fish were collected using unbaited Gee minnow traps (2 cm trap openings, 5 mm mesh) set randomly inshore of the 2-m isobath for each lake. Since fathead minnows in these lakes rarely inhabit water deeper than 2 m (Danylchuk and Tonn, unpublished data), setting traps in this habitat ensured that the probability of capture based on depth was standardized and related to the horizontal and vertical distribution of this species (He and Lodge 1990). Setting traps in random locations within the 2-m isobath during each day of the survey, by using a grid overlaid on a bathymetric map and a random number generator, ensured that marked fish were randomly distributed around each lake and that the recapture of marked fish was independent and random. In addition, Noraker et al. (1999) has shown that the distribution of marked and unmarked fathead minnows was random and independent of the site of capture and release.

From the mark-recapture surveys, estimates for males, females, and juveniles of both sexes were summed for each population in each year. Mark-recapture estimates were not biased toward underestimating population abundance since $4N_e$ was greater than the $M_n \cdot C_n$ for all populations in all years (Ricker 1975), where N_e is the population estimate, M_n is the total number of marked fish in the population on the nth day, and C_n is the total number of fish collected on the nth day when sampling for recaptures. Moreover, the abundance estimates for each population were relatively precise, with standard errors ranging from 4 to 20% (Chapter 2).

The abundance of fathead minnows in the four main study lakes varied greatly across populations and years because of differences in their susceptibility to winterkill (Chapter 2). When abundance values were converted to densities, the populations in SCL800 and SCL200 experienced the most dramatic year-over-year declines (>80%), and winterkill occurred twice in SCL800 during the 5-yr period. The population in SCL20 experienced one moderate decline (47 %), while the population density in SCL100 did not vary dramatically from year to year (Chapter 2). Thus, the four populations provided a range of variation in abundance to be incorporated into my analysis.

To generate annual estimates of relative abundance for each population, I calculated the CPUE of individual traps set each day during the mark-recapture surveys. Between 10-45 traps were set daily during the mark-recapture sampling, with the number of traps used depending on my ability to process captured fish. Traps were set in the late afternoon and retrieved the following day (duration from 15-24 hrs). The unit of effort used was number of hours each trap was set, rounded to the nearest quarter hour. As with the mark-recapture surveys, individual estimates were derived for males, females, and juveniles of both sexes, and then summed to obtain a CPUE for each trap. The CPUE for all traps was then averaged to generate a relative abundance estimate for each population in each year.

Data analysis

Data were tested for normality and homogeneity of variance with Shapiro-Wilk and Bartlett tests, respectively (Sokal and Rohlf 1995), and absolute and relative abundance estimates transformed ($\log_{10}$). When the assumptions of parametric statistics could not be met, nonparametric statistics were used.

To examine the relationship between trapping effort and abundance, Pearson correlation was used to compare the total number of fish collected, total trap nights, and total trap hours with both relative and absolute estimates. Relative and absolute abundance estimates of the four main populations were pooled and simple linear regression used to model the relationship between these estimates. I then used the resulting model to test whether the mean CPUE for the fathead minnow population in TROLS11 could generate an estimate of absolute abundance similar to that determined using mark-recapture.

All statistical analyses were performed using Statistica '99 for the PC (StatSoft Inc., Tulsa, OK, USA), and differences were considered marginally significant if $0.1 \geq P \geq 0.05$ and significant if $P \leq 0.05$.

Results

The number of fathead minnows collected during mark-recapture surveys of the four main study populations ranged from 1300 to over 31000 (Table 5-1), and from 5 to 48% of N_e. The mean number of total trap nights ranged from 72 to 261, and mean total hours set ranged from 1572 to 5485. The total number of fish collected was positively correlated with absolute and relative abundance estimates ($r=0.846$ and $r=0.814$, respectively), while total trap nights and total trap hours were negatively correlated with both estimates of abundance (absolute, $r=-0.822$ and $r=-0.817$, and relative, $r=-0.940$ and $r=-0.948$, respectively).

There was a strong relationship between absolute and relative abundance estimates for the four main study populations (Figure 5-1). The equation of the relationship between estimates was

$$\log_{10}[\text{absolute abundance}] = 4.29+0.78\,(\log_{10}[\text{relative abundance}])$$

$$R^2 = 0.801, n=20, F=72.65, P<0.0001.$$

Interestingly, the two populations with higher, less variable abundances consistently fell either above (SCL20) or below (SCL100) the regression line, whereas populations with lower, variable abundances (SCL200 and SCL800) tended to be evenly distributed around the trend line (Figure 5-1). Regardless, the relationship between absolute and relative abundance estimates had a relatively even distribution of residuals, suggesting that the nature of the relationship between estimates was not affected by population size (Zar 1996). Moreover, the relationship between absolute and relative abundance estimates was no stronger when generated separately for stable (SCL20 and SCL100) and disturbed lakes (SCL200 and SCL800).

For the survey of TROLS11, 10459 fish were collected with 10-16 traps during 7 over-night sets, totaling 94 trap nights and 1933 trap hours (Table 5-1). The mean CPUE was 5.434 fish/hr (±0.53 SE) and when this value was transformed and entered into the model generated for the four main study populations, the predicted absolute abundance was 72945 fish (95% confidence interval 55847-95499). Using the mark-recapture data for TROLS11, the absolute abundance estimate for the same period was 138234 fish (± 25412 SE, 95% confidence interval 78134-198333; Figure 5-1).

Discussion

The results of my analysis indicate that CPUE of fathead minnows can strongly reflect estimates of abundance generated via mark-recapture surveys, and, as such, CPUE could be used as a rapid, less laborious way to reliably assess spatial and temporal patterns in the abundance of fathead minnows in north-temperate lakes. In addition, the model between CPUE and estimates of abundance generated via mark-recapture surveys could be used to predict absolute abundance from CPUE, potentially increasing the scope of population studies in remote locations.

Empirical models have proven to be very useful since they can provide estimates for parameters that are usually difficult or time-consuming to measure (Dillon and Rigler 1974, Duarte and Kalff 1986). A classic example is the model derived by Dillon and Rigler (1974), in which the average summer chlorophyll *a* concentrations in lakes could be predicted from a single measurement of phosphorus at spring turnover. For fathead minnows in my study, mean CPUE similar to that calculated using all traps set during mark-recapture surveys could have been generated in only 20-40 overnight sets, which, in combination with the model between relative and absolute abundance estimates, could have allowed abundance estimates to be generated in 2-3 d, rather than the 7-9 d used for the mark-recapture surveys. However, the utility of an empirical model depends greatly on the quality of data used in its derivation, and some understanding of the causes of error associated with measured and predicted values (Dillon and Rigler 1974, Duarte and Kalff 1986).

Ideally, having some idea of the magnitude of abundance and distribution of fish prior to conducting a population survey may help optimize trapping effort and increase the accuracy of estimates (Robson and Reiger 1964), yet this may be unrealistic for surveys in remote locations or when a rapid assessment is needed (Jones and Stockwell 1995). To deal with this, the number of traps deployed on the first day of my surveys was based on the number of traps used the previous year, and I then adjusted the number of traps deployed on successive days based on current catch rates. In addition, background knowledge on general distribution patterns of fathead minnows in boreal lakes and a rough estimate of the bathymetry of the study lakes allowed me to focus trapping effort in areas where this species commonly resides.

Increasing catch rates by optimizing trapping effort during surveys may also improve the reliability of CPUE models based on mark-recapture abundance estimates (Robson and Regier 1964; Edwards et al. 1997). For instance, a CPUE model for largemouth bass, *Micropterus salmoides*, underestimated abundance by up to 89% (Edwards et al. 1997), and the large differences in abundance were attributed to the mark-recapture estimates used to generate the model since these estimates underestimated true fish abundance. As such, Edwards et al. (1997) suggested that CPUE models be derived using the relationship between CPUE and actual abundance rather than abundances estimated using mark-recapture surveys. Although this seems ideal, establishing the relationship between CPUE and actual population density may be restricted to experiments conducted in small ponds (i.e. < 1 ha), thus the transferability of such a relationship to populations in larger water bodies may be questionable if, for example, the effects of a confined distribution on the probability of capture is not considered.

Optimizing trapping effort is crucial when estimating abundance, since the accuracy and precision of estimates improves as the percentage of the population surveyed increases (Robson and Regier 1964, Edwards et al. 1997). To increase the number of marked individuals in the population and thus achieve a minimum of 5% of the estimated population size being marked, I found that the number of trap-nights needed to be greatest when abundance was low, whereas fewer trap-nights were needed when abundance was high. However, using too few trap-nights may lead to a biased estimate if areas of the waterbody inhabited by the population are not sampled (Bernard et al. 1993), or if daily patterns in catch vary due to factors such as weather (Pierce 1997). Thus, optimizing trapping effort requires striking a balance between total number of trap-nights, number of survey days, and trap distribution.

Strengthening the model by adding data from other populations could improve the accuracy of its predictions. Factors such as the presence of other small-bodied species and the morphology of the littoral zone could account for residual variance in the model because of their effects on catchability (Bernard et al. 1993, Edwards et al. 1997). In fact, littoral zone morphology may have accounted for differences in the relationship between CPUE and absolute estimates for stable and disturbed lakes. Thus, data from populations inhabiting a wider variety of lakes could reduce the confidence limits of the relationship, increase the accuracy of predicted values, and broaden the utility of this model within the region.

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Table 5-1. Trapping details and abundance estimates for fathead minnows inhabiting the four main study lakes from 1995-1999, and for TROLS11 in 1998. Numbers presented for the four main study lakes are means for the five study years ± 1 SE, with ranges in parentheses, while numbers presented for TROLS11 are for a single survey.

Lake	Number collected	Total trap nights	Total trap hours	Absolute abundance estimate	CPUE• (fish·trap^{-1}•hr^{-1})
SCL20	20575± 3068.5	81± 17.1	1572± 314.8	285075± 42824.5	14.8± 2.9
	(13617-31262)	(31-126)	(595-2254)	(168988-408836)	(8.2-22.7)
SCL100	12841± 1272.9	72± 8.4	1339± 134.9	62490± 6369.4	9.4± 0.6
	(8016-14698)	(41-92)	(822-1556)	(43881-79565)	(7.9-11.0)
SCL200	10191± 2134.2	141± 31	2919± 640.1	63127± 16070.2	5.1± 1.9
	(4350-16351)	(61-215)	(1221-4428)	(15153-96074)	(1.0-11.0)
SCL800	5384± 2484.8	261± 41	5485± 830	23490± 9829.2	1.6± 1.1
	(1300-14889)	(131-378)	(2645-7609)	(3369-59552)	(0.2-5.7)
TROLS11	10459	94	1933	138234	5.4

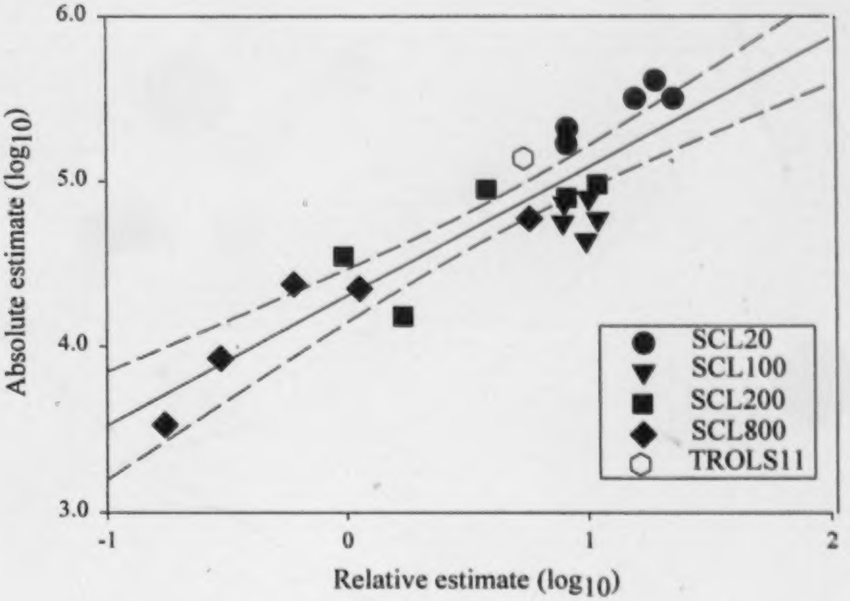

Figure 5-1 Relationship between relative ($\log_{10}$ fish·trap^{-1}·hr^{-1}) and absolute ($\log_{10}$ number of fish) abundance estimates of fathead minnows in the four boreal Alberta study lakes from 1995 to 1999, and for relative and absolute abundance estimates for TROLS11 in 1998. Note that the TROLS11 point was not included in the regression analysis. Dashed lines represent 95% confidence interval of the regression line.

Chapter 6: General Discussion

Natural disturbance is inherent in the organization of many ecosystems (Horwitz 1978; Picket and White 1985). Temporally harsh abiotic conditions that are stochastic can influence the structure of biotic assemblages, acting as a filter that allows only those organisms tolerant of such conditions to persist (Kushlan 1976; Matthews and Styron 1981; Tonn 1990). Nevertheless, even tolerant species can be adversely affected by extremely severe conditions (Klinger et al. 1982), making natural disturbance a factor that can also influence individuals within these populations (Tonn 1990). A prime example of this occurs in the western boreal region of Canada. Low winter oxygen levels common to small, shallow lakes are tolerated only by small-bodied fishes (Robinson and Tonn 1989), and my work on fathead minnows, a species common to these lakes, demonstrates that this natural disturbance also affects populations within these small-fish assemblages.

Despite their physiological and behavioural adaptations to contend with hypoxia (Chapter 1), large declines in the density of fathead minnows during my study followed winters with exceptionally low dissolved oxygen levels in lakes, indicating that winterkill can be a common and significant disturbance to populations of small-bodied fish in the western boreal region of Canada (Chapter 2). However, the extent of winter oxygen depletion among lakes and years was influenced by interacting effects of local, landscape, and regional factors that, in turn, contributed to variation in the extent and frequency of winterkill for resident fishes. Because of differences in the susceptibility to winterkill among populations and the spatial and temporal scale of my study, large declines in fathead minnow density occurred in two of five years and in three of four lakes, creating serendipitous whole-lake "experiments" that facilitated a comparison of populations before and after disturbance, and among stable and disturbed lakes. Although unplanned and loosely replicated, comparisons at this scale likely offered a more realistic assessment of the effects of disturbance on small-bodied fishes than if planned, but smaller-scale studies were conducted (Schindler 1998).

The most obvious effect of severe winter oxygen depletion is the dramatic decreases in fish abundance resulting from high, density-independent mortality (Greenbank 1945); larger individuals within populations are also often reported as more susceptible to this disturbance than smaller conspecifics, causing changes in the size structure of affected populations (Cooper and Washburn 1946; Johnson and Moyle 1969; Casselman and Harvey 1975; Fox and Keast 1991). Larger individuals generally have higher absolute oxygen demands, and, as such, succumb to winter hypoxia before smaller individuals (Moyle and Cech 1996). However, winterkill has been studied primarily in large-bodied species, and the results of my study indicate that these trends may not hold true for small-bodied fishes. In some cases, smaller individuals were more strongly affected by severe winter hypoxia than larger conspecifics (Chapter 2). Even larger individuals in small-bodied species may be small enough to capitalize on minute sources of oxygenated water, such as that associated with gas bubbles at the ice-water interface, yet larger individuals may be able to out-compete smaller individuals for access to these resources (Huntingford and Turner 1987). When the number of within-lake oxygen refugia is low, competition from larger individuals could force smaller individuals to emigrate to oxygenated tributaries in order to survive (Magnuson et al. 1985), but the success of this behaviour may depend greatly on the availability of oxygenated tributaries. For instance, although emigration was not examined in my study, only SCL200 had inflows that were accessible to fish, and these inflows may have acted as refugia for smaller individuals during periods when winter hypoxia was severe (i.e., during the winter of 1995/1996).

Interestingly, some of the same factors that can affect the extent of winter oxygen depletion (e.g., antecedent precipitation) can also influence the connectivity of tributaries to lakes. This may have been the case for SCL200 during the winter of 1998/1999, when drought and a reduction in lake levels reduced the utility of inflows as oxygen refugia, and increased the susceptibility of smaller individuals to winterkill (Chapter 2). As winter hypoxia becomes severe, the availability of oxygen refugia may also decrease for larger individuals, reducing their likelihood of survival and causing greater hypoxia-related declines in population density. Although several laboratory studies have examined how small-bodied fishes are affected by progressive hypoxia (Gee et al. 1978; Klinger et al. 1982), additional studies are needed to determine to what extent the affects are size-dependent.

High density-independent mortality resulting from winterkill can directly affect the life history of fish by reducing lifespan (Fox and Keast 1991, Chapter 3). In turn, the likelihood of survival from one year to the next can shape how an individual allocates energy among life history traits throughout its lifetime (Stearns 1992). This suggests that the shorter lifespans in populations more susceptible to natural disturbance, such as winterkill, may be related to microevolutionary selection (Van Winkle et al. 1993). For example, Reznick et al. (1996) demonstrated that different levels of mortality experienced by guppies, *Poecilia reticulata*, contributed to the selection of certain life history traits, including lifespan.

However, in habitats where the level of mortality is variable because of stochastic disturbance, selection may favor the evolution of phenotypic plasticity, which allows individuals to maximize fitness for a wide range of environmental conditions (Stearns 1992). This may be the case for the fathead minnow, as variation in life history traits observed during my study of natural populations is consistent with predictions for organisms in highly variable and unpredictable environments (Stearns 1992). In addition, manipulative experiments showed that the timing of reproductive activity in male fathead minnows is plastic and can be modulated by population structure and its affects on social status (Chapter 4). Specifically, small males advanced their reproductive condition, held nesting territories, and spawned earlier in the reproductive season only when large males were absent or removed from the population (Chapter 4). Although changes in population structure during these experiments were inconsistent with changes observed for natural populations (Chapter 2), the release from social inhibition may still occur if the absolute number of larger individuals is sufficiently reduced following winterkill (personal observations), even if the relative abundance of large individuals increases. Additional manipulative experiments could help determine the extent that population density, in combination with size structure, affects social interactions, status-dependent selection, and the extent of plasticity in reproductive traits for fathead minnows. Such experiments could also lead to more realistic predictive life history models by identifying factors that can influence the expression of traits and evolution of adaptive strategies

(Gross 1996), but are usually hard to measure in natural populations (Reznick et al. 2002; personal observations).

Plastic life history traits possessed by species tolerant to disturbance may not only help increase individual fitness, but such flexibility, in combination with a short generation time, can increase the intrinsic rate of increase of the population. Such plasticity facilitates population recovery following catastrophic events, and thereby promotes persistence and resilience in these highly stochastic environments (Stearns 1992; Begon et al. 1996; Symes and Jones 1999). The ability of survivors to capitalize on reduced competition for resources and adjust their allocation of energy among the competing ends of maintenance, growth, and current reproduction can facilitate increased production of young who can in turn also benefit from reduced competition resulting from disturbance (Murnyak et al. 1984; Chapter 3). In the absence of large, socially dominant individuals, small males were able to spawn and produce comparable total numbers of offspring as were produced in treatments in which large males were present (Chapter 4).

The offspring of these uninhibited small males were smaller at the end of the growing season than the young of large males (Chapter 4), which differed from what was observed in natural populations, where age-0 fish in lakes prone to winterkill grew faster and to a larger body size than age-0 in more stable lakes (Chapter 3). The high population density used in this experiment, however, in combination with greater competition for food resources among similar sized conspecifics (Vandenbos 1996), may have contributed to the results in the experimental ponds. Further investigations into the indirect effects of winterkill on density-dependent and size-dependent relationships that influence the expression of life history traits and the ability of fathead minnows to respond to this disturbance should provide additional insight into the mechanisms responsible for natural variation in population-level traits of small-bodied fishes in north-temperate regions.

Winterkill-mediated patterns in population density of small-bodied fishes may help explain other natural patterns in northern aquatic ecosystems (Paszkowski and Tonn 2000; Zimmer et al. 2001). For example, re-colonization of a prairie wetland by fathead minnows following winterkill affected primary production and the abundance of macroinvertebrates (Zimmer et al. 2001). In addition, Eaton et al. (unpublished data) found that the abundance of young-of-the-year wood frogs (*Rana sylvatica*) increased dramatically following winterkill of small-bodied fishes. Given that wood frogs recruit from lakes to riparian and upland areas where they become part of the forest food web, variability in the density of small-bodied fishes could thus affect terrestrial systems as well. Natural patterns in the abundance of small-bodied fishes could also affect avian species that are a part of lake ecosystems, whether through competition for food resources (Duffy 1998) or via the availability of prey for piscivorous birds (Gingras and Paszkowski 1999). Relationships between small-bodied fishes, aquatic invertebrates, and piscivorous birds could, in turn, affect other patterns in lake ecosystems, such as dynamics in the parasite fauna (Dobson and May 1987; Giles 1987; Sandland et al. 2001). Clearly, winterkill as a natural disturbance has the potential to affect many components of boreal lake ecosystems, especially where small-bodied species dominate fish assemblages, not unlike the many direct and indirect effects of fire on adjacent or surrounding forest ecosystems (Gresswell 1999; Tonn et al. 2003).

Understanding the incidence of natural disturbance and its cascading effects through ecosystems can also be important for examining the potential impacts of human disturbance (Gresswell 1999; Schindler 2001). For example, although forest harvesting occurred in the catchments of my study lakes after two years of monitoring, any ability to detect an effect of this disturbance was partially limited by the high natural variation in density of fathead minnows in the lakes over these two pre-harvest years. Given the natural frequency and severity of winterkill, in fact, post-hoc power analyses indicated that 3 to15 yr of pre-harvest data would have been necessary to detect a 50% decrease in minnow density caused by forest harvesting with a level of significance of 0.05 (Zar 1996).

Despite the inability of my study to formally detect an impact of forest harvesting, several of the factors that I identified as playing an important role influencing the natural susceptibility of lakes to winterkill (Chapter 2) can also be affected by forest harvesting (Schindler et al. 1990; Carignan et al. 2000) and other human disturbances that occur in this region (Cooke and Prepas 1998; Schindler 2001). However, partitioning out the effects of human disturbances from natural patterns may be difficult, especially when the temporal scale of natural disturbance exceeds the period in which such systems are usually studied. In my case, five field seasons, in combination with the availability of a 15 yr data set and results from manipulative experiments in small ponds, contributed greatly to the conclusions I was able to make regarding the natural incidence and effects of winterkill in the Boreal Plains. Similarly, a combination of long-term studies, large-scale empirical surveys, and small-scale manipulative studies may be useful for deciphering the effects of human disturbance in this system. Although a somewhat daunting task, empirical models, such as the one I derived for CPUE and absolute population estimates (Chapter 5), can help make the process of detecting the effects of human disturbances on fish assemblages in the Boreal Plains more efficient and more likely. Alternatively, given that the susceptibility to winterkill is based on a predictable set of local and regional environmental factors (Chapter 2), efforts should be made to protect more sensitive lakes by limiting human activities that augment natural disturbance regimes in northern lake ecosystems.

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